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THE ROLE OF COLUMBIAN GROUND SQUIRRELS IN TWO SUBALPINE MEADOWS IN SOUTHWESTERN ALBERTA

by

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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The Role of Columbian Ground Squirrels in two Subalpine Meadows in Southwestern Alberta submitted by Steven Blemmer Carroll in partial fulfilment of the requirements for the degree of

I dedicate this thesis to the late Dr. Albion "Doc" Hodgdon, who nurtured my interest in the plant world, and took me to the mountains for the first time.

ABSTRACT

Two subalpine meadows inhabited by Columbian ground squirrels (*Spermophilus columbianus columbianus*) were studied: 1) to provide a comparison of microclimates, soils, plant communities, plant production, plant phenology and ground squirrel populations; 2) to document the occurrence and relative abundance of plant taxa on and off ground squirrel burrow mounds; and 3) to provide a descriptive environmental analysis of Columbian ground squirrel habitat in the hope that animal behaviorists and ecologists can better interpret their observations.

The study sites were both at 2225 m asl on the Mt. Allan complex (50^{0} 58' N 115^{0} 12' W) in the Front Range of the Alberta Rocky Mountains. One site (Marmot) was on a south-facing slope in an east-facing cirque. The other site (Wind Creek) was on level ground in a north-facing cirque.

Wind Creek is cooler and windier than Marmot, and receives less global radiation. Summer precipitation did not differ between sites. Vapor pressure deficits at Marmot were less due to damp soil.

Five plant communities were delimited at Marmot: Snowbank, *Epilobium*-*Bromus*, *Juniperus*-*Arctostaphylos*, Wet forb and Mesic grass. These were correlated with topography, drainage patterns and snowdepth and snowmelt patterns. Aboveground vascular plant standing crop was 125 and 238 g dry wt m^{-2} for the first two communities, respectively. Mean vascular plant cover ranged from 68% to 97%.

Three plant communities were delimited at Wind Creek: *Potentilla*-*Achillea*-sedge, Mixed forb-sedge and Mixed forb-*Salix nivalis*. These communities had 87%, 95% and 89% mean vascular plant cover, respectively,

and aboveground vascular plant standing crop of 116 and 112 g dry wt m^{-2} in the last two communities, respectively.

The Columbian ground squirrel population at Marmot increased from three adults in 1975 to five adults and three juveniles in 1976. At Wind Creek, seven adults and three juveniles occupied the site in 1976, resulting in a density of 0.002 m^{-2} (vs. 0.005 m^{-2} at Marmot in 1976).

The Wet forb and Mesic grass communities at Marmot contained no burrows, and were little used by squirrels. The Snowbank, *Juniperus-Arctostaphylos* and *Epilobium-Bromus* communities are all used for burrow sites, but most feeding occurs in the latter. Standing crop samples in paired excluded and non-excluded plots located in all but the Wet forb community gave higher values in plots accessible to squirrels. It is believed that these differences are a result of altered microclimate. Squirrels at Wind Creek spend more time feeding in the *Potentilla-Achillea*-sedge and Mixed forb-sedge communities than in the Mixed forb-*Salix* community. This results from increased numbers of burrows in the former two, where increased microtopography and surface rocks provide preferred burrowing sites.

No unique plant species occur on burrow mounds. The most important colonizers are *Epilobium*, *Bromus* and *Fragaria virginiana*, all three of which spread vegetatively. Species assemblages on these mounds are more uniform than those of the surrounding meadow matrix, indicating a more uniform microenvironment. Mound assemblages are not floristically dependent on the plant community in which they occur. Wire-mesh exclosures on two actively used mounds showed the importance of ground squirrels as a source of mortality to colonizing plants.

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Many fellow graduate students in the Departments of Botany and Zoology have shown an active interest in this work and their comments and companionship have made this demanding course of study worthwhile.

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INTRODUCTION

During the last decade, plant ecological studies in the Canadian Rocky Mountains have increased steadily. These studies have concentrated either on plant communities within defined geographic areas, or on particular vegetation types over an extensive area, and have emphasized forest systems.

Except for alpine studies, only Stringer (1973) concentrated on non-forest vegetation in his study of low elevation grasslands. He discussed two subalpine grassland types which occur between 1375 and 1675 m in Jasper and Banff National Parks, Alberta. Both of these types, the Stipa richardsonii* grassland and the Elymus innovatus shrub savanna, occur in small, isolated pockets within the matrix of subalpine forest.

Hettinger (1975) described two subalpine meadow habitat-types from the Vine Creek drainage basin in Jasper National Park. A Salix glauca/ Elymus innovatus community occurred on a fossil lake bed at 1670 m, and a lush Salix vestita/Poa alpina community occurred at about 2000 m within glacial cirques. These communities are similar to those described by Beder (1967) and Trottier (1972) in Snow Creek Valley, Banff, and Highwood Pass, respectively.

Herb-dominated communities have received little attention, but have been described by Kuchar (1973) in Waterton Lakes National Park, Alberta. He describes five chionophillic meadow community types occurring between 1675 and 2500 m. A lush, species-rich moist forb community type is dominated by Phleum alpinum, Valeriana sitchensis,

Erigeron peregrinus, *Achillea millefolium*, *Castilleja rhexifolia* and *Potentilla diversifolia*. This community type resembled the *Thalictrum occidentale* association described by Trottier (1972). A Rock forb community type is floristically similar to the Moist forb type, but has much lower cover, little soil development and many xerophytic species. A Dry meadow community type is characterized by turf mosses (*Polytrichum piliferum* and *Tortula ruralis*), *Selaginella densa* and sedges. A *Xerophyllum* community which is nearly a monoculture, is prevalent in drier parts of the park. Finally, an Intermediate meadow type occurs on north-northeast aspects, and includes a mixture of alpine and prairie species.

Beder (1967) described an *Elymus innovatus* association which occurs on steep south-facing avalanche slopes in Snow Creek Valley, Banff. This association has a moderate snow cover and a chernozemic alpine turf soil.

Kirby and Ogilvie (1969), Trottier (1972) and Jaques et al. (1974) describe a limited number of subalpine grass and sedge dominated communities from the Kananaskis-Highwood Pass area. These communities will be described in the following chapter.

The term "subalpine" has had various interpretations. Love (1970) reviews the historical development of the use of this term, and proposes that it be applied to the area or zone above and adjacent to continuous, upright forest (50% canopy cover). This corresponds to the forest-tundra ecotone. This classification includes high elevation spruce-fir forest in the montane zone, in contrast to the authors cited above. Rowe (1972) delimits the East Slope Rockies subalpine zone

(SA.1) as that portion of the east slopes characterized by the dominance of Engelmann spruce (Picea engelmannii), Engelmann X White spruce (P. glauca) hybrids, subalpine fir (Abies lasiocarpa) and lesser amounts of other conifers. This is also the interpretation used in this study.

The rugged fault-block nature of the Canadian Rocky Mountains results in limited areas of high elevation grasslands and herbfields. The limited extent of these areas may prove to be one of their most critical features, since herbivores (especially ungulates and rodents) rely heavily on such areas for both summer and winter grazing.

Studies on the behavior and socio-ecology of small mammals in the foothills and mountains have been conducted quite independent from plant ecological studies. Recent studies by Steiner (1970a, 1970b, 1971, 1972, 1973, 1974), Kivett (1975), Betts (1976) and Michener (1977) have made important contributions to our understanding of the individual and social behavior of Columbian ground squirrels. Attempts to interpret the adaptiveness of individual behavior and social systems have been hampered in part by our lack of understanding of the environment which these rodents inhabit (Betts 1973).

The present study concentrates on the primary producer and abiotic components of two subalpine meadows which are inhabited by Columbian ground squirrels (Spermophilus columbianus columbianus). By understanding some of the biotic and physical parameters operative in these meadows, a better understanding of the interaction of these animals and their environment may be achieved.

The two most important actions of Columbians in respect to vegetation are grazing and burrowing. Columbians eat a wide range of plant species

at these sites, and characteristics such as net production, standing crop and seed set might be expected to show the influence of this herbivory. Through their burrowing activities, Columbians have both direct (burying) and indirect (microhabitat modification) effects on the vegetation. Studies conducted during 1975 suggested that burrowing activities were more important than herbivory in these meadows. Therefore research concentrated on the former during 1976.

The immediate effects of the burrowing actions of these squirrels are to kill living plants and create localized sites of disturbance. In this respect, Columbians can be considered natural agents of disturbance, and can be classed with other such agents as fire, avalanche, blowouts and soil frost activity. These agents are natural, but not totally predictable in time or space. They may all be interpreted as causing cyclic changes in plant and animal populations by periodically interrupting succession. Several workers (e.g. Osburn 1958, Bryant and Scheinberg 1970, Heinselman 1973) have used this interpretive approach in studying disturbance, and their work is compared to the Columbian ground squirrel - subalpine meadow system (see Discussion).

With this background, the objectives of this study can be summarized:

(1) To provide a comparison of microclimates, soils, plant communities, plant production, plant phenology and Columbian ground squirrel populations for two subalpine meadows in the Front Range of the Alberta Rocky Mountains.

(2) To document the occurrence and relative abundance of plant taxa on and off ground squirrel burrow mounds.

(3) To provide a descriptive environmental analysis of Columbian ground squirrel habitat in the hope that animal behaviorists and ecologists can better interpret their observations.

Nomenclature follows the following authors, unless otherwise stated: Moss (1959) for vascular plants; Crum (1973) for mosses; and Hale (1969) for lichens. Voucher specimens are deposited in the University of Alberta herbarium, Edmonton, Alberta (ALTA).

DESCRIPTION OF STUDY AREA

GEOLOGY AND GEOMORPHOLOGY

Mt. Allan is situated in the Front Ranges of the Alberta Rocky Mountains, which consist of several subparallel thrust sheets or fault blocks, each overriding its eastern neighbor. Because of this faulting (thrusting), portions of some sheets are secondarily deformed (Osborn and Jackson 1974). Volumetrically, the most important rocks in the Front Ranges are Mississippian and Devonian formations, consisting principally of resistant dolomite and limestone (Rutter 1972). Because these Paleozoic rocks are relatively resistant, they stand out in relief against topographic lows formed from less resistant rock types. The many steep cliffs throughout the Front Ranges are composed of these resistant carbonates. Examples within the immediate area are Mts. Bogart, Kidd and Loughheed (Figure 1).

In contrast to these Paleozoic carbonate cliffs, topographic lows consist mainly of shales, sandstones and siltstones of Mesozoic age (Rutter 1972). These rock types are mainly clastic, and not as resistant as those previously discussed (Osborn and Jackson 1974). Farther west, the Main Ranges of the Rockies consist primarily of Cambrian carbonates and quartzitic sandstone (Rutter 1972).

More specifically, Mt. Allan lies within the Lac des Arcs thrust plate, in the immediate footwall of the Mt. Rundle fault. Because of the fault block nature of this area, the towering carbonate cliffs of the Mt. Rundle fault rise above the much lower trough of Mesozoic formations; both structures trend northwest to southeast. This 81 km long trough has been discussed in detail by Crockford (1949). It is

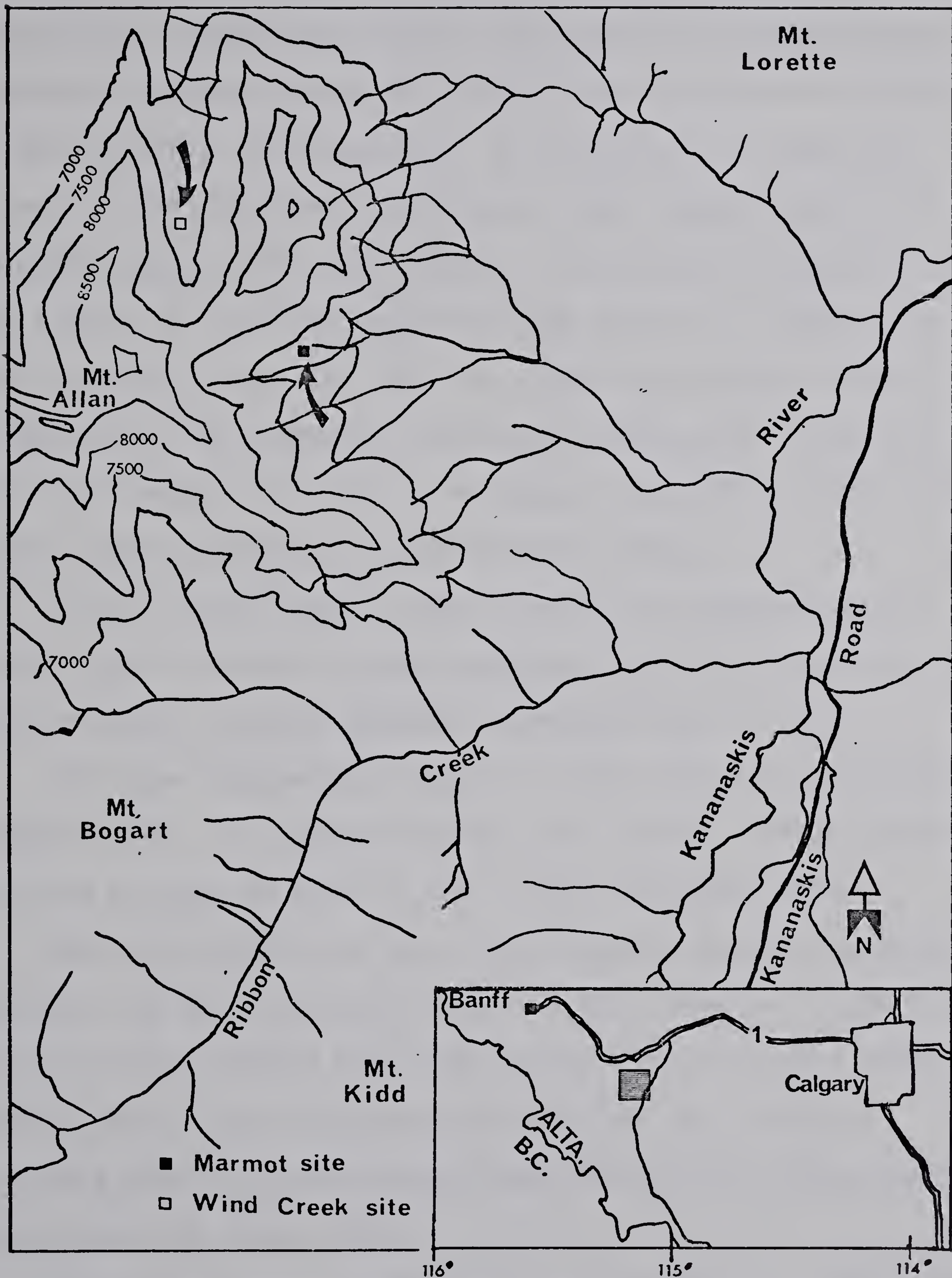


Figure 1. Location of study sites, 80 km west of Calgary.

essentially synonymous with the Cascade Coal Basin, named for the relatively large reserves of coal found in one of its formations (Norris 1957, Jones and Bielenstein 1971). The trough is an assymmetrical to overturned syncline (Norris 1971), and has been referred to by Norris (1957), as the Mt. Allan syncline. To the west of the trough lie several of the higher peaks in the area: Mts. Lougheed, Bogart and Kidd, The Wedge, and Mt. Evans-Thomas. To the east lie Pigeon Mountain, Mt. Lorette, Mt. McDougall and Fisher Peak (Figure 1). Alone of all the surrounding peaks, Mt. Allan lies within this trough, causing a slight bend in its otherwise relatively straight course. Because of this relationship, Mt. Allan is the highest peak (2791 m) in the area which exposes non-paleozoic rocks (Crockford 1949).

"It [Mt. Allan] probably owes its origin and preservation to a thick capping of massive, weather-resistant conglomerates and to a well-developed synclinal structure" (Crockford 1949, p. 12).

This upper conglomeratic capping has been designated the Blairmore Formation (Fm). Its maximum thickness on Mt. Allan is 305 m, but at one time may have been as thick as 1005 - 1980 m (Crockford 1949).

Below the Blairmore Fm lies the coal-bearing Kootenay Fm, which underlies the entire Cascade Coal Basin. This formation is totally exposed on the northeast face of Mt. Allan, where it is 936 m thick (Norris 1957). This formation was divided into four members by Crockford (1949), but later authors have reduced this to three (Norris 1957, Osborn and Jackson 1974).

The uppermost member, which abuts the Blairmore Fm, is designated the upper sandstone and conglomerate member. It is 576 m thick, and cliff-forming. The middle 345 m thick member, designated the shale

member, contains most of the mineable coal seams in the area. The lowest member (15 m thick), designated the basal sandstone member, is a persistent, grey, cliff-forming sandstone. This formation overlies the Fernie Fm (Norris 1957).

According to Crockford (1949), the Kootenay Fm is a freshwater deposit, the exception being the basal sandstone bed of the basal sandstone member. This particular bed is considered to be of marine origin as it is continuous with the sandstone at the top of the Fernie Fm, in which marine fossils have been found. He speculates that Kootenay sediments were probably deposited in freshwater lakes and swamps located near the sea. The source of these sediments was the higher land to the west. Fossils from Kootenay deposits in the Crowsnest Pass area were given a Lower Cretaceous age by Sir J.W. Dawson (Crockford 1949). Norris (1971) indicates that these deposits are of Late Jurassic and early Cretaceous age. Although less resistant than the Paleozoic carbonates, the Blairmore and Kootenay Fms are more resistant than the deeper Fernie and Spray River Fms (Crockford 1949).

To this point, local physiography has been described in terms of rock types and mountain-building phenomena, with topography resulting from the interaction between endogenic forces that have uplifted the land, and exogenic forces which have, and still are, wearing it down. The most recent unlift occurred during the Miocene, and since that time, exogenic processes have been dominant. The two factors which have been most influential in this downwearing have been erosion through runnoff of precipitation and streamflow, and glaciation.

Several authors have investigated the extent and affects of Pleistocene glaciation within the area. Stalker (1973) and Osborn and

Jackson (1974) cite evidence for four glacial advances within the Kananaskis valley. Both geomorphic and depositional evidence are available for the two younger advances, but only the former is available for the two older advances. The four advances represent a series of decreasing magnitude from oldest to youngest. Based on stratigraphic evidence, the minimum age of the final advance is given as 11,000 yrs BP. A similar sequence of four glacial advances of decreasing magnitude has been postulated for the Bow River valley by Rutter (1972). He has designated the second advance as the Bow Valley advance, which is said to have retreated to the present townsite of Banff before readvancing (Canmore advance or Bow Valley readvance). Subsequently, extensive deglaciation occurred so that few cirques still contained ice at the beginning of the Eisenhower Junction advance. This small advance represented the last major appearance of ice within this portion of the Bow River valley (between Eisenhower Junction and Seebe).

Stalker (1973) suggested that the last ice advance in the Kananaskis Valley corresponds to the Canmore advance of the Bow Valley, and may date from 12 - 10,000 BP. Shaw (1972) however, has indicated that problems exist in correlations which have been made, for instance, between Bow Valley advances and those in the U.S. Rockies. Because of the proximity of the Bow and Kananaskis Valleys, correlations are probably justified despite these cautions.

Osborn and Jackson (1974) indicate that the third advance in the Kananaskis Valley probably achieved an approximate surface elevation of 1700 m in the Barrier Lake area, and that it may have extended beyond the mouth of the valley. The amount of retreat before the final advance, which may have penetrated as far as Barrier Lake, is unknown.

Stalker (1973) has suggested that the cirques formed in the lower Kananaskis Valley (which presumably includes the Marmot cirque) probably developed at the time of the first ice advance, although an absolute date is not offered. Neoglacial activity in these cirques is indicated as follows: "The freshness of the materials in the high cirques (at about 7500 to 8000 feet asl) in the southwestern part of the area (in Sec. 16 and 21 of Tp. 23, Rge. 9) indicates that these cirques were reoccupied by ice during the Neoglacial " (Stalker 1973, p. 24). It should be noted that the cirque in Sec. 16 of Tp. 23, Rge. 9 is the Marmot cirque.

Since the glacial period and excluding neoglacial activity, fluvial and mass wasting processes have been dominant, and have contributed to the present-day geomorphology of these areas. Osborn and Jackson (1974) have discussed these and other surficial processes in some detail.

SOILS

The distribution and nature of soil types found in these valley systems have been investigated by several workers. Crossley (1951) described the soil types found within the subalpine zone of the Kananaskis Forest Experiment Station. Surface deposits in this area were found to be largely unconsolidated, and included glacial till, transported deposits of alluvial and lacustrine origin, and residual and sorted residual deposits. Podzolization was considered the dominant soil forming process in the area, although the calcareous parent material tended to retard this process somewhat. He found the following five profile types to be most important: alluvium, chernozemic, rendzina, brunisolic and podzolic.

Karkanis (1972) investigated soil types over a larger portion of the Kananaskis Valley and described profiles belonging to six orders: Regosols, Brunisols, Luvisols, Podzols, Chernozems and Organics.

Beke (1969) studied the soils of three experimental watersheds in Alberta, including the Marmot Creek Basin. Glacial till was found to be most common surficial deposit in the basin, with an average thickness of 6.1 to 12.2 m. This till, which was derived from valley glacial action, is light brownish grey, silty and calcareous, and contains large amounts of dolomitic limestone, sandstone and quartzitic rock fragments. Local Mount Allan till occurs at higher elevations (including the Marmot cirque). It is generally neutral to weakly acidic and contains large amounts of platy and flaggy rock fragments.

Well drained soils within the basin showed vertical zonation. Grey Luvisols (especially Brunisolic Grey Luvisols) were common at lower elevations. Somewhat higher, Ferro-Humic Podzols became most important. Dystric Brunisols, which formed the largest soil zone in the basin, replaced these at even higher elevations. In the highest portion of the basin, Regosols became the most important soils.

Brunisolic soils were placed in either the Dystric or Eutric Great Group. Degraded Dystric Brunisols were found immediately above the Ferro-Humic Podzol zone. Alpine Dystric Brunisols were found in the vicinity of treeline, and were characterized by a Chernozemic-like Ah horizon. This soil type was divided into two classes. Class A types occurred under Larix lyallii vegetation, and were characterized by well-developed moder-type Ah horizons, poorly-expressed eluviation, a dark B horizon and evident accumulation of Fe and Al. They were found to be similar to Arctic Brown soils in Alaska as described by

Tedrow *et al.* (1958). Class B types were found under *Kobresia bellardii* vegetation, and were characterized by a well-developed moder-type Ah, and a chernozemic-like B (versus a Brunisolic-like B horizon in the Class A type).

Degraded Eutric Brunisols were found to occupy minor areas within the Dystric Brunisol zone, especially on steep slopes of drainage pathways. These were characterized by a weakly-developed (or absent) Bm horizon.

Orthic and Cumulic subgroups of the Regosolic Order were recognized. Cumulic types commonly occurred under grass vegetation, and had deep, non-chernozemic Ah horizons.

Several characteristics of well-drained soils were observed to change with elevation. Factors which decreased included the following: profile expression, total carbon content in the L-H horizon, weathering of clay minerals, illuviation of colloids and pH and density of the B horizon. Those factors increasing with elevation included: pH uniformity througout the profile, total nitrogen content, total exchange capacity, total carbon content of the B horizon, total carbon and nitrogen content of the A horizon and total exchange capacity of the A horizon.

Greenlee (1974) has studied the soils of Bow Valley Provincial Park and adjacent areas within the Kananaskis watershed. These low-elevation studies emcompassed an area of 27 km^2, and resulted in a soils map. Like the study by Karkanis (1972), six soil Orders were recognized. In common between these two studies were soils of the Regosolic, Brunisolic, Luvisolic, Organic and Chernozemic Orders. In contrast was Karkanis' recognition of Podzolic soils and Greenlee's recognition of Gleysolic

soils. Parent materials recognized by Greenlee included loess, lacustrine deposits, gravel, alluvial sediment, sand, glacial till, shale, sandstone and peat.

These combined studies show the great variability in profile development characteristic of mountainous environments. The good correlation between soil type and plant community type found by Knapik, et al. (1973) show the importance and value of soils work in studies of plant communities.

CLIMATE

Previous work done in mountain valley systems has made it clear that significant changes in climatic parameters over short distances are commonplace. Factors such as the dimensions and orientation of the valley, the rise of terrain above the valley floor, the slope, and the aspect of the terrain are thought to be the primary factors controlling valley climate. Secondary controls include permanent ice and snow fields, water bodies, soils and vegetation (Lester 1974). Because each one of these factors differs between the Bow and Kananaskis Valleys, climatic patterns also differ significantly. The Bow Valley is larger, is oriented east-west (in the region of the study areas) and is more highly modified by man (greater urbanization, more roads and highways, scattered industrial operations, etc.). The Kananaskis Valley is smaller, is oriented north-south, and is less modified by man, (the most important exceptions being the forestry trunk road and the Barrier Lake, Upper Kananaskis Lake and Lower Kananaskis Lake reservoirs). Because of the complexity of mountain valley climatic patterns, few generalizations can be offered. Lester (1974) has briefly described

climatic patterns for the Kananaskis Valley, and his treatment is here summarized. Extension of these patterns to the Bow Valley system should be done with caution.

On the basis of available data, the Kananaskis Valley can be classified as cold snowforest (microthermal) because the mean temperature of the warmest month is above 10^{O}C, and that of the coldest month is below -3^{O}C. Summers are cool, the mean temperature of the warmest month being below 22^{O}C, and there are less than four months with mean temperatures of 10^{O}C or more. As one moves south, away from the valley mouth, temperature decreases and precipitation increases. This same pattern occurs with increasing elevation.

Because of the location of these valleys, air masses from both the Arctic and the Pacific Ocean are important, causing a large range in temperature. Several aspects of temperature are summarized in Table 1. Areas both within and outside of the Kananaskis Valley are included for comparison. Comparison between the Environmental Sciences Centre (ESC), Marmot Creek Basin (MCB) and the Kananaskis fire lookout tower (KLO) show the effects of elevation. Unexpectedly high mean minimum temperatures at KLO are probably best interpreted as nocturnal cold air drainage. MacHattie (1970) investigated the occurrence of inversions on a transect between Mt. Allan and Mt. McDougal, and concluded that inversions occurred almost every night. He found inversions as large as 9-18^{O}C in the lower 30.5 m of relief. (See Results for a discussion of inversions on a local scale within the Wind Creek cirque.)

Precipitation also shows dramatic differences between stations (Table 2). ESC has significantly more precipitation than Banff, both during the summer (June through August totals) and on an annual basis.

Table 1. Mean annual, mean maximum, mean minimum and mean daily temperatures (^{o}C) for selected months at four stations.

Station and Elevation (m)	Years of Record	Jan	May	June	July	Aug	Annual
Environmental	1941-70	-3.3[1]	+13.8	+17.4	+22.1	+20.7	+9.4
Sciences		-9.7[2]	+ 7.1	+10.7	+14.1	+13.1	+2.7
Centre (ESC)		-16.0[3]	+ 0.3	+ 3.8	+ 6.1	+5.5	-3.9
(1390 m)							
Marmot	1963-72	-7.9	+10.2	+14.8	+18.9	+19.6	+6.1
(CON 5) (MCB)		-13.0	+ 4.1	+ 8.5	+11.7	+12.1	+0.2
(1770 m)		-18.1	- 2.1	+ 2.2	+ 4.4	+ 4.6	-5.8
Kananaskis	1964-70			+12.4	+17.8	+16.1	
Lookout (KLO)				+ 7.9	+12.1	+10.8	
(2080 m)				+ 3.1	+ 6.4	+ 5.6	
Banff	1941-70	-11.3[2]	+ 7.6	+11.3	+20.1	+13.5	+2.3
(1384 m)							

1 mean maximum
2 mean daily
3 mean minimum

Table 2. Mean monthly and mean annual precipitation (mm).

Station	Years Of Record	May	June	July	August	Annual
ESC[1]	1941-70	82	116	64	70	648
BRS[2]	1963-70	64	137	38	41	-
KLO[1]	1964-70	-	102	59	71	-
BANFF[1]	1941-70	51	65	48	48	477
MCB[1]	1963-76	70	106	53	54	658

[1] See table 1 for station location and elevation

[2] Boundary ranger station, Kananaskis Valley, 1460 m ASL

Maximum precipitation for all stations occurs in June. This results from the northward movement of the Polar Front across this area in late spring, causing an increase in eastward-moving extratropical cyclones from the Gulf of Alaska. Increased convective activity also contributes to this precipitation maximum (Lester 1974).

Although summer precipitation at KLO was slightly less than that at ESC, Ferguson and Storr (1969) have documented a positive correlation between precipitation and elevation in Marmot Creek Basin. Between 1964 and 1968, they recorded a mean precipitation value of 625 mm at approximately 1700 m, and a mean value of 1125 mm at approximately 2300 m. Although snow can occur in any month, it is relatively rare during the summer on the valley floor, but not at all rare at the highest elevations. For example, on 12 June 1976, approximately 15 cm of snow fell on the Wind Creek and Marmot study areas.

Like temperature and precipitation, wind varies considerably on a local basis. Direction and intensity of wind are both highly influenced by local topography and elevation. Exceptionally large increases in wind speed occur at and above treeline (Storr 1973). Measurements taken at ESC show the predominance of southwesterly winds at that location. Although dominant winds at higher elevations to the west and south are from the southwest and northwest quadrants, valley orientation and local relief modify this pattern.

On days with weak macroscale flow, vertical mixing of air is minimal. At these times, local circulation is more pronounced. In work done between Mt. Allan and Mt. McDougal, MacHattie (1968) has shown the occurrence of a counter-clockwise shift in wind direction due to

differential heating of east aspects in the morning, and west aspects during the afternoon.

One of the more interesting phenomena related to wind is the chinook. These warm, dry gusty winds originate to the west as Pacific air masses move across the Continental Divide and lose their moisture on west-facing slopes. Longley (1967) has investigated the frequency of chinooks in Alberta, and has determined that a zone of maximum occurrence occurs east of the Divide, its exact location depending on local and regional physiography. Based on data from provincial weather stations, Longley constructed a map with isolines of equal occurrence of winter chinooks (defined as the number of days with temperatures greater than 3.9^{0}C). Table 3 is based on this information. Although some of this variability can be attributed to differences in elevation, and hence expected differences in temperatures, nevertheless, a clear pattern emerges. Table 4 examines chinook occurrence for several stations along a transect running west-east. Of the four stations examined, ESC has the greatest frequency of chinooks. Although Exshaw is only 13 km away, it shows a marked decrease in chinook occurrence. Thus, the Kananaskis Valley lies on or near the above-mentioned zone of maximum chinook frequency.

Chinooks may be important to the biota in several ways. These warm winds increase evapotranspiration during all seasons, and may lead to dessication of the vegetation. Chinooks may contribute to the incidence and magnitude of fires, both directly, and indirectly through their dessicating action. At the same time, they may act to disperse seeds and spores. During the winter, these winds melt the snow, and transport particles of snow and ice, contributing to the maintenance

Table 3. Mean number of days during December, January and February with temperatures >3.9°C (from Longley 1967).

Location	Years Of Record	Number Of Days
Banff	34	9.8
Exshaw	34	19
Jasper	29	14
Kananaskis	25	29
Lake Louise	34	2.9
Waterton HQ	13	28
Calgary	35	27

Table 4. Mean number of days during December, January and February with temperatures >3.9°C for several stations along a west-east transect.

Location	Elevation (m)	Distance From Kananaskis	Number Of Days
Banff	1384	45 km W	9.8
Exshaw	1298	13 km W	19
ESC-Kananaskis	1390	-	29
Calgary	1049	65 km E	27

of winter snow-free areas. Such areas on Mt. Allan are used extensively by Rocky Mountain Big Horn Sheep for winter grazing (Jaques pers. comm.).

Patterns of global insolation are quite predictable. Maximum and minimum radiation occur in July and December respectively, resulting directly from the elevation angle of the sum. The most significant deviation from expected radiation patterns based on solar position occurs in June, when a "shoulder", or lower than expected value occurs. This results from increased cloudiness in June, and is correlated with precipitation data.

By means of summary, Table 5 presents temperature and precipitation summaries, by month, for two weather stations, one within the Kananaskis Valley (ESC) and one within the Bow Valley (Banff). These serve to indicate the temperature and precipitation regimes at relatively low elevations within these valleys. For a discussion of microclimate at selected high elevation sites, see Discussion.

VEGETATION

Few detailed vegetation studies have been conducted within the area. Kirby and Ogilvie (1969) described the forest structure of Marmot Creek Basin. Kirby (1973) also described the forest inventory on the Kananaskis Forest Experiment Station to the north and east of the study areas. Trottier (1972) investigated the alpine vegetation of the Highwood Pass area, which forms the divide between Pocaterra Creek, a tributary of the Kananaskis River, and the Highwood River to the south. Baig (1972) conducted a more extensive study in his investigation of timberline vegetation in the Rocky Mountains of Alberta. Jaques *et al.* (1974) have summarized these studies as they relate to the Kananaskis

Table 5. Mean monthly and mean annual temperature (^{o}C) and precipitation (mm) for the Environmental Sciences Centre (ESC) and Banff. Values are based on the 30 year period 1941-1970.

Month	ESC Temperature	ESC PPT	BANFF Temperature	BANFF PPT
January	-9.7	28	-11.3	33
February	-6.1	35	- 6.8	30
March	-4.2	38	- 3.8	23
April	1.8	63	2.4	36
May	7.1	82	7.6	51
June	10.7	116	11.3	65
July	14.1	64	20.1	48
August	13.1	70	13.5	48
September	9.3	52	9.1	38
October	5.0	40	4.2	36
November	-2.3	29	-3.8	35
December	-6.2	30	-8.8	34
Year	2.7	648	2.8	477

Valley, and have supplemented these with observations of their own.

The planimetric area of the Kananaskis River watershed is approximately 93,020 ha. Of this, 38% is forested and 10% is alpine. The remaining portion consists of water bodies, rock and talus, meadows, shrublands, cleared lands and alluvial fans. Of the forested areas, 89% is seral, dominated largely by Pinus contorta (lodgepole pine). Only 11% of forested areas, or 4% of the valley is under climax or near climax forest (Jaques et al. 1974).

This seral situation reflects the past importance of fire. Three major fires have occurred in this century. In 1910, approximately 2590 km^2 were burned, including southern portions of the Kananaskis Valley. In 1919, a considerable area around the Kananaskis Lakes burned. The most extensive fire occurred in 1936. In that year, major portions of the entire watershed were burned, as were very large areas elsewhere in the Pacific Northwest. This largely accounts for the widespread importance of lodgepole pine today, as it is an aggressive post-fire species throughout the Rockies. Jaques et al. (1974) cite 43 fires as having occurred since 1958 in the Kananaskis Valley, burning ca. 365 ha.

Nearly all forest stands in the valley can be classified as either Upper Foothills Boreal (B.19c) or East Slope Rockies Subalpine (SA.1) after Rowe (1972). A few scattered stands at low elevations in the area of confluence between the Bow and Kananaskis Rivers can be classified as Douglas Fir and Lodgepole Pine Montane (M.5).

Rowe (1972) distinguishes between the first two of these forest types by the presence of pure white spruce (Picea glauca) in the former,

and white spruce - Engelmann spruce (*P. engelmannii*) hybrids and pure Engelmann spruce in the latter. Daubenmire (1974) has shown that this is not the case, as a wide band or zone of introgression occurs between these spruce species. Based on several specimens from the Kananaskis Valley which were analyzed for hybridization, introgression appears to be widespread (Jaques *et al*. 1974). Perhaps a better distinction would include consideration of the hybrid index score of spruce in addition to the relative importance of subalpine fir (*Abies lasiocarpa*).

Subalpine stands within these valleys are characterized by the dominance of Engelmann X white spruce and subalpine fir. As mentioned, lodgepole pine is also important, either in association with the above species, or in pure stands, especially at lower elevations. Lodgepole also occurs sporadically as high as treeline, where krummholz forms can sometimes be found.

Jaques *et al*. (1974) described fifteen subalpine forest types from the Kananaskis Valley. These stands are dominated alternately by Engelmann X white spruce, subalpine fir, alpine larch (*Larix lyallii*) and combinations of these. Understory changes occur in response to elevation, drainage, soil type, aspect and other environmental factors. In their description of forest types within the Marmot Creek Watershed Research Basin, Kirby and Ogilvie (1969) describe ten timber habitat types (productive forest stands) and ten alpine habitat types (non-productive forest types and herbaceous and shrubby stands above timberline). Of the 924 ha comprising the Basin, 52% is in timber and 48% is in alpine habitat types. The single most important habitat type in the Basin is the *Picea-Abies/Menziesia-Lycopodium* habitat type, which comprises 24% (224 ha) of the total area. This type occurs at mid

elevation (approximately 1678 - 2044 m) on well-developed podzolic soils. Canopy species include hybrid spruce, subalpine fir and an occasional lodgepole pine. A dense tall shrub layer is comprised mainly of *Menziesia ferruginea*, *Rhododendron albiflorum*, *Sorbus sitchensis* and *S. scopulina*. Species of *Vaccinium* (*V. myrtillus*, *V. membranaceum* and *V. scoparium*) form a low shrub layer. Herb and bryophyte strata are dominated by *Lycopodium annotinum*, *Pyrola uniflora*, *P. secunda* and *Arnica latifolia* and *Pleurozium schreberi*, *Hylocomium splendens*, *Dicranum* spp. and *Peltigera aphthosa*, respectively.

The next most important timber habitat type is the *Picea-Abies/Vaccinium scoparium* type, which comprises 12% (107 ha) of the Basin. This type extends from timberline (2196 - 2257 m) to about 2044 m where it adjoins the *Picea-Abies/Menziesia-Lycopodium* type. Low shrubs include *Vaccinium scoparium*, *V. myrtillus*, *Phyllodoce glanduliflora* and *P. empetriformis*. Important herbs include *Arnica latifolia*, *Potentilla diversifolia* and *Pedicularis bracteosa*; *Dicranum fuscescens*, *Barbilophozia* sp. and *Cladonia* spp. are important bryophytes and lichens. *Larix lyallii* occurs in this type at higher elevations.

Alpine habitat types include meadow vegetation in addition to krummholz - *Vaccinium scoparium*, shrub types of *Salix* and *Phyllodoce*, and rock and talus types. Most important of these are *Phyllodoce* types (14% - 129 ha), *Carex* - *Antennaria* types (13% - 116 ha) and rock and talus types (12% - 110 ha). Meadows comprise 32% (292 ha) of the Basin total. These alpine types range from very wet *Salix* stands with deep snowcover and high groundwater levels to mesic south-facing meadows of *Danthonia* and *Deschampsia*, to dry, snow-free stands of *Dryas octopetela* and *Kobresia bellardii*.

Trottier (1972) has described ten alpine plant associations from the Highwood Pass area. He divides these into low, mid and high alpine zones. The low alpine zone, which occurs from the valley bottom (2135 m) to approximately 2290 m, includes associations dominated by *Salix barrattiana*, *Deschampsia caespitosa* and *Thalictrum occidentale* with scattered stands of *Carex nigricans* and *Phyllodoce*. The mid alpine zone (2290 - 2440 m) includes associations dominated by *Salix arctica*, *Salix nivalis*, *Carex nigricans*, *Cassiope tetragona*, *Dryas octopetela* and *Kobresia bellardii*, with some higher-extending *Phyllodoce* associations. The high alpine zone occurs from about 2590 to 3050 m.

Jaques *et al*. (1974) integrated the studies by Kirby and Ogilvie (1969) and Trottier (1972) and arrived at twelve alpine plant associations in addition to rock, talus and avalanche sites. Talus slope vegetation is currently under study by Kershaw and Gardner (Kershaw pers. comm.).

Non-alpine meadows have received very little attention in these areas. Occasional mention is made of the occurrence of alpine vegetation types below treeline, attributed by Trottier (1972) to the occurrence of temperature inversions. Kirby and Ogilvie (1969) describe a *Calamagrostis* habitat type at low elevations which they correlate with soil too shallow to support trees. Jaques *et al*. (1974) describe a *Carex* - *Deschampsia caespitosa* association which occurs in very moist depressional areas within the subalpine zone. Similar areas of hummocky topography support a *Carex* - *Deschampsia* association in depressions and an association of *Betula glandulosa*, *Deschampsia*, *Phleum alpinum*, *Fragaria virginiana*, *Bromus inermis*, *Trisetum spicatum* and *Poa leptocoma* on topographic highs. Subalpine meadows have wider occurrence than their degree of treatment indicates, and more detailed investigations would

be desirable.

Detailed vegetation studies in the portion of the Bow River Valley under consideration have not been published.

METHODS

VEGETATION ANALYSIS

Vegetation composition and pattern were documented at both the Marmot and Wind Creek sites, in August 1975 and August 1976 respectively. In sampling at Marmot, the site was first subdivided into arbitrary sections based primarily on topography. Horizontal rows, running parallel to the slope and to each other, were established at one meter intervals. Because sections were not of constant size, the number of rows varied. Each row was next divided into contiguous 50 cm units to correspond to the larger dimension of 20 x 50 cm quadrats, the number of units depending on the width of the particular section. Quadrats were then randomly selected so that each row within a section had an equal number of quadrats, and a 1.6% sampling intensity of the site was achieved.

Within each of the 241 quadrats analyzed, percent crown cover for each species was estimated. This procedure generated both cover and frequency data. The design of this sampling scheme allows interpretation of the data in several ways. First, quadrat information can be combined in order to obtain an overall impression of vegetation within the study area. Second, quadrats can be grouped according to subjectively delineated plant communities in order to generate detailed comparative information for each. And finally, quadrats within rows can be grouped to generate information on changes over well-defined mesotopographic gradients (sensu Billings 1973). Subsequent analysis will consider each of these approaches.

Sampling procedures in the Wind Creek site were quite similar to those outlined above. Because of topography, two transects were

established which radiated away from the central pond and bissected the site in an east-west direction. Quadrats (n = 40) were placed at random in relation to these transects. Based on previous experience, increased familiarity with the vegetation and time-constraints, sampling intensity of the Wind Creek site was approximately .08%. This may have resulted in a less-than complete species list for the site but periodic collections throughout the summer uncovered most species not included within quadrats. It is relevant to note that only one species was found in the Marmot site during the 1976 field season which had not been recorded there during the previous summer.

Burrow mound vegetation was sampled independently, and necessitated modified procedures. Because mound "porches" are roughly circular in outline, and quite variable in size, the 20 X 50 cm quadrat was deemed inadequate. Instead, a circular quadrat with a diameter of 25 cm was used, eliminating mounds smaller than 25 cm from the sampling. For those mounds sampled, the circular quadrat was centrally located. When possible, two or three non-overlapping quadrats were used on a mound. Cover was estimated for each species and the number of individuals was counted.

Subsequent to this analysis, the following observations and measurements were made on each mound sampled: mound dimensions, dimensions of burrow entrances, aspect of the mound and plant community of the surrounding vegetation.

PHENOLOGY

Phenological observations were made in an attempt to compare plant development between the two sites, and between different communities

within a site. To this end, five 1.5 X 1.5 m permanent plots were established - three at Marmot and two at Wind Creek. Within these plots, observations were made on vegetative development and time of flowering and fruiting. Rather than deal with specific individuals, observations were based on the phenological stage of the majority of individuals within a species. This allowed a crude time-sequence of events to be constructed for several of the more important species. Observations were made at approximately weekly intervals.

NET PRIMARY PRODUCTION

Estimates of plant production were made through periodic harvesting of above-ground biomass. In an attempt to assess impact of the Columbians on production, six paired plots were established at Marmot during the 1975 growing season. These were located in a variety of plant communities, but in all cases, were located in relatively homogeneous areas. Each of these pairs included one plot accessible to squirrels, and an exclosure plot constructed of 1 X 1 cm wire mesh. It should be noted that these exclosures also served to exclude other vertebrate herbivores. Each of these twelve plots contained ten 20 X 50 cm quadrats which could potentially be harvested, each separated from neighboring quadrats by a 20 cm buffer zone to minimize the influence of an adjacent harvested quadrat.

For each of five harvestings, five plot-pairs were randomly selected. Single quadrats were then randomly selected within each plot, and above-ground biomass was clipped at ground level and separated into several categories: several key species were harvested separately in an attempt to note selective feeding behavior; mosses and lichens were also dealt

with separately. Depending upon conditions, separation was done either in the field or the laboratory. Samples (green living and brown current year) were oven-dried at $80^{\circ}C$ for a minimum of 48 hr, and weighed.

Based on information gained during 1975 (see Results), it was decided that a repeat of the procedure was not warranted during 1976. Instead, two larger non-exclosed plots were established at both sites. For each harvesting period, three 20 X 50 cm quadrats were randomly selected from each plot. Plant material within each quadrat was then separated into four categories (graminoids, forbs, mosses and lichens), oven-dried and weighed. Periodic harvesting (n = 4) within these plots allowed comparison of production between the two sites (for the 1976 growing season). No indication of utilization by squirrels was determined.

SOIL PROFILES AND SOIL MOISTURE

Three soil pits were dug at each site to describe profiles in representative plant communities. Profile descriptions included delineation and measurement of horizons, with the following parameters observed or measured for each horizon: color (Oyama and Takehara 1967); texture (The System of Soil Classification for Canada, 1974, p. 226); structure; consistency; root abundance, size-class distribution, orientation and distribution within peds; boundary distinctness and form; pH (Hellige-Truog Soil Reaction (pH) Tester No. 693); and reaction with HCl.

The gravimetric method of soil moisture determination was used in order to compare soil moisture in different plant communities. Samples

were taken three times at each study site during the 1976 season. At both Marmot and Wind Creek, four sites were chosen for these samples, and subsequent sampling was confined to these four sites. In each case, two replicates were taken at three depths: 0-5, 5-10, and 10-15 cm. Cores were placed in pre-weighed soil tins. After wet weight was determined, the soil was dried at 105°C for 72 hr, and reweighed.

In addition to moisture content, soil moisture available to plants was also determined. Percent moisture at 1/3 and 15 bars of pressure was determined with soil pressure plates for composite samples of the 0 to 5 cm and 10 to 15 cm depths at all eight soil moisture sites (see above). Available soil water was calculated using the soil moisture desorption curves.

MICROMETEOROLOGY

Micrometeorological measurements were made at both the Marmot site (1975 and 1976) and the Wind Creek site (1976), and included information on air temperature, relative humidity, global short-wave radiation, mean wind speeds and precipitation.

Air temperature and relative humidity were measured continuously by a Belfort No. 5-594 hygrothermograph calibrated against a mercury thermometer and a Bendix aspirating psychrometer. Data were recorded between 4 July - 1 September 1975 at Marmot, and between 23 May - 29 August 1976 and 31 May - 28 August 1976 at Marmot and Wind Creek respectively. These instruments were placed in 50 X 38 X 38 cm wooden frame shelters with aluminum side louvres; shelters were placed level the ground and secured by guy lines. From these data, mean maximum, mean minimum and mean daily temperatures were determined over seven

day periods, the latter calculation based on readings every six hours. Also in each shelter was a Taylor #5458 maximum and minimum registering thermometer to serve as a check against readings by the hygrothermograph. Relative humidity data were extracted at six hour intervals, and converted to vapor pressure deficit (VPD) as follows:

$$\log_{10} e_s = 0.02604\ T + 0.82488 \qquad (1)$$

$$e = \frac{(RH)\ (e_s)}{100} \qquad (2)$$

$$VPD = e_s - e \qquad (3)$$

where e_s = the saturation vapor pressure at temperature T (^{o}C), e = actual vapor pressure and RH = relative humidity (Rosenberg 1974, p. 131).

Global short-wave radiation was measured with a Belfort No. 5-3850 A pyrheliograph (pyranometer). Readings were continually taken between 22 June - 29 August 1975 and 23 May - 30 August 1976 at Marmot, and between 25 May - 28 August 1976 at Wind Creek. In all cases instruments were placed upon the hygrothermograph shelters, with the sensors located .48 m above the ground surface.

Wind was recorded by means of a Belfort No. 5-349A 3-cup totalizing anemometer. Mean wind speed between readings was determined by dividing the miles of wind passage by elapsed time. Anemometers were placed with the cups approximately 0.6 m above the ground surface, and were secured by guy lines.

Precipitation at Wind Creek was measured by a Taylor 2701-M Clear Vu circular rain guage. Precipitation measurements at Marmot were taken with a copper standard rain guage by the Atmospheric Environment Service,

Hydrometeorological Branch, Environment Canada.

BURROW MOUND PLANT DYNAMICS

Several approaches were used to describe some of the short-term changes occurring in species assemblages on burrow mounds. These methods allowed both qualitative and quantitative interpretations of changes occurring over two growing seasons. The use of small wire-mesh exclosures on active burrow mounds provided information on the effects of squirrels on these changes.

These exclosures (0.2 X 0.2 X 2 m) were placed on two of three active burrow mounds in 1975 and provided comparative information on growth and survival of individual plants on portions of mounds protected from squirrels and portions subjected to squirrel activity. These paired plots were mapped twice during 1975 (3 July and 27 August) and twice during 1976 (10 July and 14 August).

Periodic mapping and photographing of mounds and continual observations contributed to an understanding of burrow mound plant dynamics.

COMPARISON OF MEADOWS

RESULTS

Physical Features

Both study sites are on the flanks of the Mt. Allan complex (Tp. 23, R. 9) in the Front Range of the Alberta Rocky Mountains, approximately 80 km west of Calgary and 11 km south of the Trans-Canada Highway. Although the two sites are at the same elevation (2225 m), and on identical parent geologic material (Kootenay Formation shale and sandstone), important differences exist.

The 1500 m^2 Marmot site is on a south-facing slope in an east-facing cirque. This cirque contains the headwaters of Middle Fork Creek, a tributary of Marmot Creek. Marmot Creek flows east into the Kananaskis River, which is a tributary of the Bow River to the north. The Marmot Creek watershed is designated Marmot Creek Basin, and has been the site of intensive hydrometeorologic research over the past 15 years (Department of Energy and Mines, 1963-1974).

The 5000 m^2 Wind Creek site is on the floor of a larger, north-facing cirque. Sub-surface drainage enters Wind Creek, a tributary of the Bow River. Although the two sites are separated by only 2 km, a steep ridge rises between them. This ridge connects the main peak of Mt. Allan, to the southwest, with a slightly lower peak (locally called Mt. Collembola) to the northeast. At its lowest point, this saddle reaches approximately 2530 m. Figure 1 shows the location of these features and the two sites.

The origin of these cirques lies in Pleistocene glaciation, and

neoglacial activity has subsequently reworked these areas (Stalker 1973). Other geomorphic processes have been important during the last several thousand years. Freeze-thaw cycles in the soil have resulted in extensive areas of patterned ground, especially soil stripes. Rock fall from the slopes above occurred continually throughout the 6.5 months spent in the field. Winter snow activity was evidenced by avalanche-destroyed woodland observed during the spring of 1976 in both cirques. Erosional processes continue to play an active role through surface runoff and stream channel formation. All these processes, perhaps in addition to others, have combined to shape these cirques, and have had both direct and indirect effects on the biota.

SOILS

Three soil pits were dug at each study area in order to investigate variability in soil characteristics in different plant communities. At Marmot, one soil pit was excavated in each of the Snowbank, *Epilobium* - *Bromus* and *Juniperus* - *Arctostaphylos* communities. Soil profiles were quite similar in these three pits, the most significant differences being texture and thickness of the B horizon. Beke (1969) has classed similar profiles from within the Marmot Creek watershed as Alpine Dystric Brunisols. Horizon characteristics are outlined in Table 6. These profiles show fairly well-differentiated L-F-H, A, B, and C horizons, with only one BC transition. Color is generally dark brown to black. All horizons had a fine granular structure, with friable or very friable consistency. Roots were mostly very fine (0.075 - 1.0 mm) and except for the Snowbank community, reached into the C-horizon. Horizon boundaries were almost exclusively clear and wavy.

The Snowbank site had the thickest profile (70 cm to the B-C boundary), due to an exceptionally thick B horizon (56 to 64 cm). This profile also had the lightest-colored C horizon. The *Epilobium*-*Bromus* profile had the only BC transition horizon, which resembled the C horizon in texture and consistency, but had a slightly higher chroma (10 YR 2/3 vs. 10 YR 2/2). Only the *Juniperus*-*Arctostaphylos* soil profile had a charcoal layer, which occurred at the A-B boundary and was 2.5 to 5.0 cm thick.

At Wind Creek, two pits were dug in mesic, level communities, and one was dug in a north-facing *Cassiope tetragona* community. Horizon characteristics for these profiles are summarized in Table 7. Profiles

Table 6. Soil profile characteristics of three soil pits, Marmot.

Plant Community (Depth to C Horizon)	Horizon	Color	Texture	Structure	Consistency	Roots	Boundary	Thickness (cm)	pH
Epilobium-Bromus	H	Br-Bl				few fine, abundant very fine, abundant micro	clear, wavy	3.8- 6.4	6.1
(47.0 cm)	A	Bl	SL	fine granular	v. friable	very few fine abundant very fine	clear, wavy	8.9-11.4	7.0
	B	Dk Br	LS	fine granular	friable	very few fine abundant very fine	clear, wavy	12.7-15.2	7.0
	BC	Br-Bl	SCL	fine granular	v. friable	abundant very fine	clear, wavy	16.5-19.1	7.0
	C	Br-Bl	SCL		v. friable	abundant very fine			7.1
Juniperus-Arctostaphylos	H	Bl						5.1- 7.6	
(41.9 cm)	A	Br-Bl	SiCL	fine granular	v. friable	abundant very fine very few fine	abrupt, smooth	5.1- 7.6	5.5
	B	Dk Br	SiL	fine granular	v. friable	abundant very fine	clear, smooth	27.9-30.5	5.5-6.0
	C	Br-Bl	SiC			few very fine			5.5-6.0
Snowbank	H	Bl					clear, wavy	2.5- 5.1	
(69.9 cm)	A	Br-Bl	SiCL	fine granular	v. friable	abundant very fine	clear, wavy	3.8- 7.6	5.0-5.5
	B	Br-Bl	SiC	fine granular	v. friable	plentiful very fine		55.9-63.5	6.5
	C	Dull Yel-Br	SiC		v. friable	none			7.0

terminology after The System of Soil Classification for Canada (1974)

Table 7. Soil profile characteristics of three soil pits, Wind Creek.

Plant Community (Depth to C Horizon)	Horizon	Color	Texture	Structure	Consistency	Roots	Boundary	Thickness (cm)	pH
Mixed forb-sedge	H	Bl				few fine abundant very fine	abrupt, smooth	5.1- 6.4	6.0
(74.3 cm)	A	Br-Bl	SC	fine and medium granular	v. friable	plentiful fine plentiful very fine	clear, smooth	8.9-11.4	6.2
	B_1	Dk Br	HC	fine granular	friable	very few fine few very fine	gradual, wavy	15.2-22.9	5.8
	B_2	Dk Br	SL	fine granular	v. friable	very few fine plentiful very fine	clear, smooth	15.2-20.3	5.9
	B_3	Dk Br	SC	fine granular	v. friable	none	clear, smooth		
	C	Dk Br	Sl			none			
Mixed forb-*Salix*	H					very few medium few fine		2.5- 3.8	6.0
(73.7 cm)	A	Br-Bl	SiCL	fine granular	friable	plentiful very fine very few medium	clear, smooth	10.2-12.7	6.0
	B_1	Dk Br	SiC	fine granular	v. friable	very few fine few very fine	clear, smooth	15.2-17.8	5.9
	B_2	Dk Br	SL	fine granular	v. friable	few very fine	abrupt, smooth	22.9	6.0
	B_3	Br-Bl	L	fine granular	v. friable	few very fine	gradual, wavy	16.5-22.9	6.0
	C	Br-Bl	S			none			6.2
Cassiope	H					very few medium	clear, wavy	5.1- 8.9	6.1
	A	Bl	Sil	fine granular	friable	few fine plentiful very fine	clear, wavy	10.2-15.2	5.9
	B_1	Bl	L	fine granular	v. friable	plentiful very fine	clear, wavy	10.2-12.7	5.7
	B_2	Bl	L	fine, medium and coarse granular	v. friable	very few very fine	clear, wavy	19.1-22.9	6
	C		S			none			5.4

terminology after The System of Soil Classification for Canada (1974)

here were much more complex than at Marmot, with deeper profiles and two or three B horizons each. Horizon structures were granular with a friable to very friable consistency. Again, texture and rooting patterns varied considerably. Boundary characteristics were also more variable at this site.

The soil pit in the Mixed forb-sedge community had the deepest profile and a very complex B horizon. The B_3 horizon, which contained a significant amount of clay, was sandwiched between two horizons of sandy loam texture. The profile in the Mixed forb-*Salix nivalis* community also had three B horizons, but had less clay than the former. The *Cassiope* community profile contained very little clay and a variable amount of sand. Color throughout was black, and structure was granular. Mottling occurred in the lower B horizon. Size of roots varied between very fine and medium, but tended to be smallest in the Mixed forb-sedge community. In no case did roots reach the C horizon. Boundaries between horizons were consistent in the *Cassiope* profile (clear, wavy) but showed significant variability in the other profiles. Soil ph showed little variability, but was slightly more acidic under the heath-dominated vegetation of the *Cassiope* community.

In general, soil profiles were better developed at Wind Creek. Although A horizons were comparable between sites, B horizons at Wind Creek were much thicker than at Marmot (48.7 cm vs. 37.7 cm). Texture tended to be more coarse at Wind Creek, especially in the C horizon. Structure and consistency varied little between and within sites.
In no case did a horizon show any reaction when tested with HCl, indicating a lack of carbonates.

In addition to soil profile descriptions, percent soil moisture was also determined at each site. These measurements were taken at three depths at each of four sites within each study area. These samples allowed comparisons within, but not between study areas.

At Marmot, samples were taken in the snowbank, Epilobium-Bromus and Juniperus-Arctostaphylos communities and from a large burrow mound with little plant cover. Trends in water content were consistent on the three sample dates. At all but the burrow mound site, highest water content occurred in the 0 to 5 cm zone (Figure 2a). Values dropped sharply in the 5 to 10 cm zone, and less sharply in the 10 to 15 cm zone. The Epilobium-Bromus community consistently had the highest water content, followed by the snowbank and Juniperus-Arctostaphylos communities. The burrow mound had a markedly different pattern of soil water, since the 0 to 5 cm zone had very low water content. Water content increased in the 5 to 10 cm zone, and decreased again at 10-15 cm.

Trends in available water were less erratic than those for water content (Table 8). Available water in the 0 to 5 cm zone at Marmot varied only from 8.15 to 9.75% between the four communities.

Trends in soil water at Wind Creek were comparable to those at Marmot, but less consistent. Samples were taken from the Mixed forb-sedge and Mixed forb-Salix communities, from a Dryas octopetela dominated community and from a burrow mound. The first three generally showed a trend of decreasing water content with depth, as at Marmot

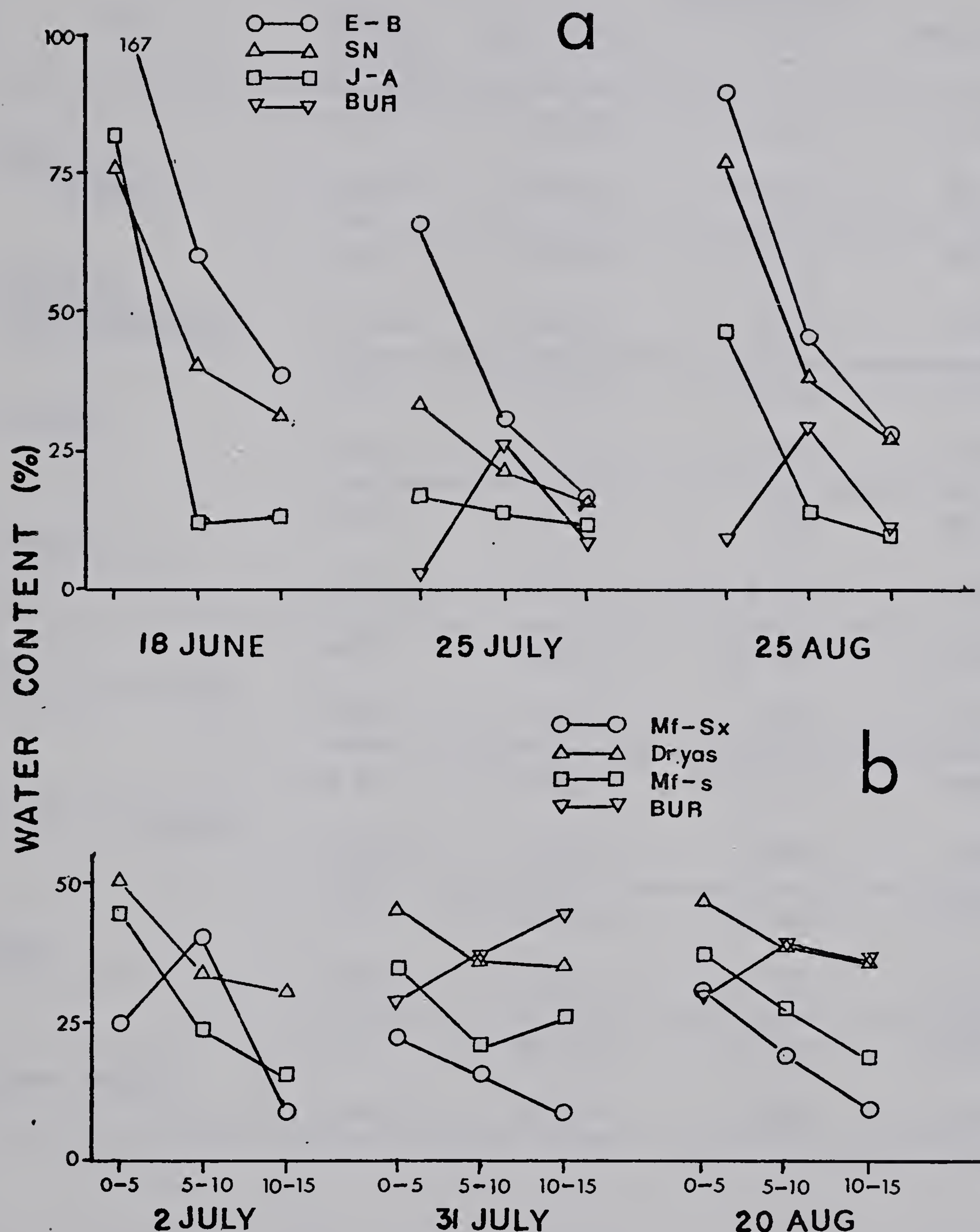


Figure 2. Soil moisture (%) of a) the Epilobium-Bromus (E-B), Juniperus-Arctostaphylos (J-A) and Snowbank (SN) communities and a burrow mound at Marmot, 1976, and b) the Mixed forb-sedge (Mf-s) and Mixed forb-Salix (Mf-Sx) communities, a Dryas dominated community (Dryas) and a burrow mound at Wind Creek, 1976 (n=2, at three depths (cm)).

Table 8. Soil moisture characteristics at Marmot and Wind Creek.

Site	Depth (cm)	Moisture (%) 1/3 Atmos.	15 Atmos.	Available
Epilobium-Bromus	0-5	42.49	33.19	9.30
	10-15	21.21	13.10	8.11
Juniperus-Arctostaphylos	0-5	21.48	13.33	8.15
	10-15	18.12	8.26	9.86
Snowbank	0-5	31.36	21.61	9.75
	10-15	15.12	11.91	3.21
Burrow mound	0-5	15.91	7.54	8.37
	10-15	16.49	6.67	9.82
Mixed forb-sedge	0-5	22.37	13.24	9.13
	10-15	17.83	9.36	8.47
Mixed forb-Salix	0-5	22.14	12.15	9.99
	10-15	9.58	6.06	3.52
Dryas	0-5	28.05	15.14	12.91
	10-15	28.83	13.53	15.30
Burrow mound	0-5	26.69	15.78	10.91
	10-15	32.37	15.40	16.97

(Figure 2b). Water content of the burrow mound had lowest values between 0 and 5 cm, increased in the 5 to 10 cm zone, and in one case (31 July) increased, in the other case (20 August) decreased slightly in the 10 to 15 cm zone. Unlike the burrow mound at Marmot, the Wind Creek mound had water contents comparable to those in the other three sites. This mound had been recently enlarged and contained much loamy material, which would increase the water-holding capacity of the soil. Available water again was fairly consistent in the 0 to 5 cm zone (9.13 to 12.91 %) but more variable in the 10 to 15 cm zone (3.52 to 16.97 %) (Table 8). As at Marmot, water content was near or above field capacity in nearly all cases.

Although available water is relatively constant for a given portion of a soil profile, water content is very sensitive to climatic parameters, especially precipitation. During the two week period prior to the 31 July reading, 49.0 mm of rain fell at Wind Creek; during the two weeks prior to the 20 August reading, 40.6 mm fell. As water content measurements were not taken on a regular (e.g. weekly) basis, it should not be assumed that plants were never subject to water stress, especially on exposed, coarse-textured burrow mounds. The burrow mound at Marmot for example was below the permanent wilting point (-15 bars) in one case (0 to 5 cm zone on 25 July) and below field capacity in the other three cases (10 to 15 cm zone on 25 July and 0 to 5 and 10-15 cm zones on 25 August). The remaining soil zones tested at Marmot were either above, or in a few cases, slightly below field capacity.

MICROCLIMATOLOGY

Temperature

Temperature data have been summarized for weekly intervals. Figure 3 shows mean maximum, mean minimum and mean daily (based on readings taken at 6 hr intervals) temperatures for both sites during 1975. Figure 4 shows this same information for the summers of 1975 and 1976 at Marmot.

Comparing the two sites, it is evident that Marmot is consistently warmer than Wind Creek. This temperature differential is relatively small early in the season, but increases markedly such that by late August, mean maxima at Wind Creek are approximately equal to mean daily at Marmot, and mean daily at Wind Creek are approximately equal to mean minima at Marmot. In no case is a value for Wind Creek greater than the corresponding one for Marmot. All six curves show similar seasonal trends. Minimum temperatures occurred during the week of May 30th in all cases. Temperature then increased markedly during the following week, and then again during late June and early July. Temperatures peaked during the same week (18 July), and subsequently showed an erratic, but generally decreasing trend until the end of the measurement period.

Data from two summers at Marmot indicate a somewhat less erratic trend during 1975. Maximum values for 1975 occurred at least two weeks earlier than in 1976, and except for the mean minimum, were much greater than 1976 values. Temperatures then declined through the end of August, lacking the dramatic increase of early August, 1976.

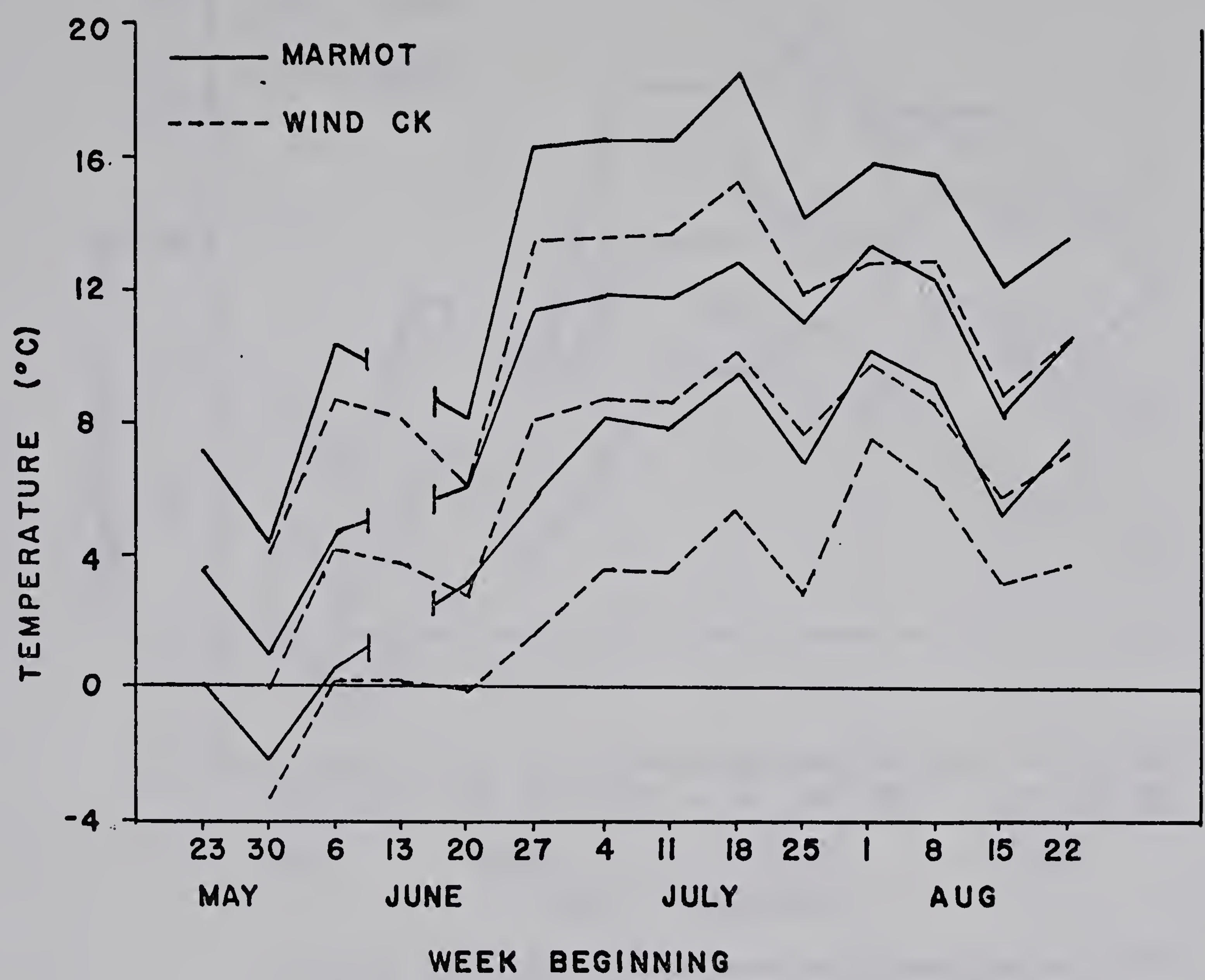


Figure 3. Mean weekly maximum, mean and minimum temperature (°C, 15 cm above ground) at Marmot and Wind Creek, 1976.

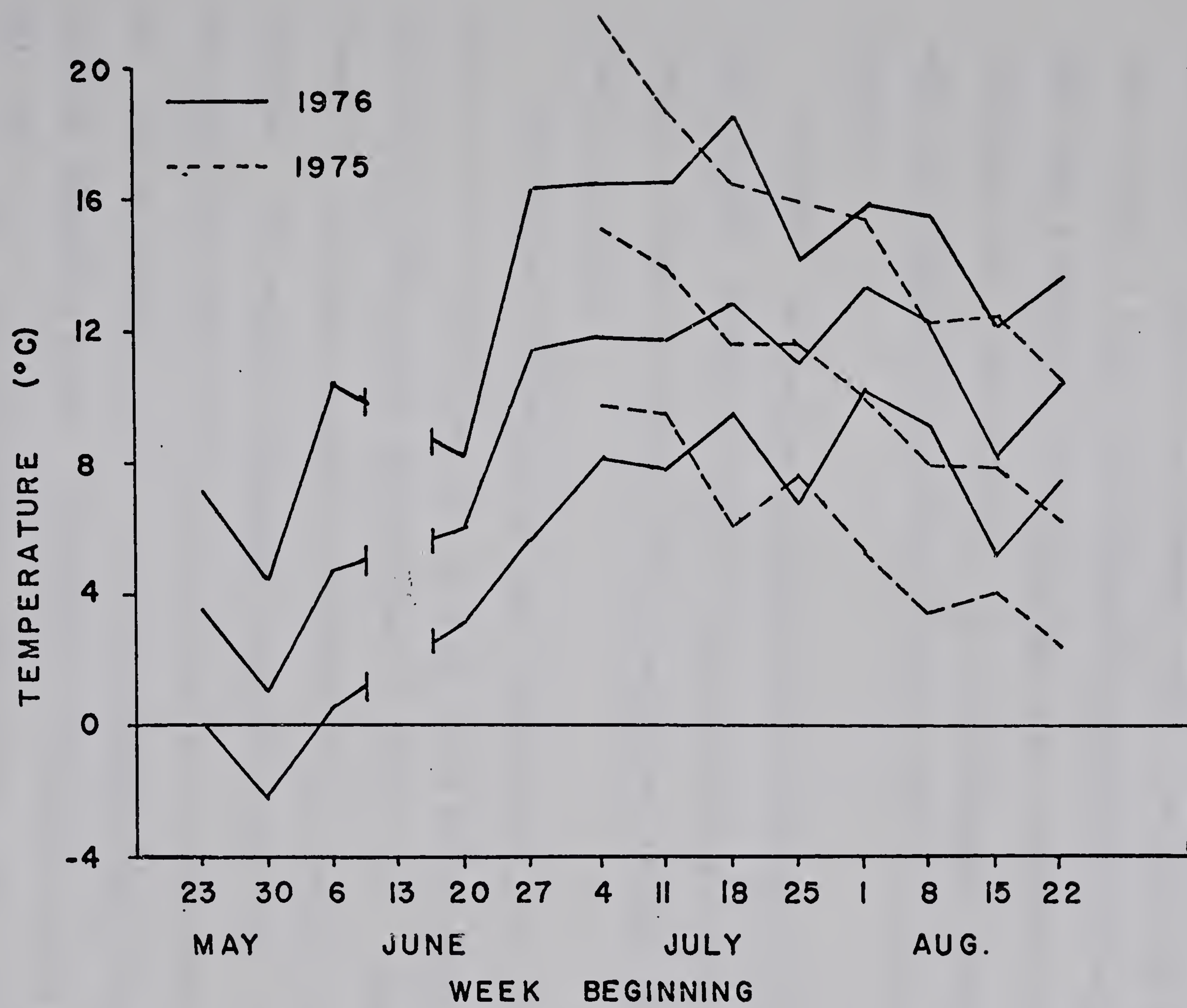


Figure 4. Mean weekly maximum, mean and minimum temperature (°C, 15 cm above ground) at Marmot, 1975 and 1976.

Some insight into this comparison can be gained by referring to Table 9, which compares monthly mean temperature and total precipitation for 1975 and 1976 to 30 year normals (1941 - 1970) at two weather stations. These data indicate that July 1975 was considerably warmer than average, with June and August being somewhat cooler. The very high mean values for the week of 4 July 1975 reflect this unusually warm month. The lower than average July 1976 values may have contributed to this contrast. The August trend seen in Figure 4 is also reflected by Table 9. Whereas August 1975 was cooler than average, August 1976 was somewhat warmer than average.

To answer the question of whether cold air drainage takes place in these cirques, minimum air temperatures at various elevations have been compared. Figure 5 compares minimum temperatures at four sites in the Wind Creek cirque.

One site was located on the west (east-facing) wall at 2290 m (#1), one was on the cirque floor (#2, at study site) and two were on the east wall, one at 2285 m (#3), and the other at 2360 m (#4). Although these curves do not portray a totally consistent trend, a pattern can be observed. The lowermost thermometer on the east wall (#3), located 58 m above the study site, had minima equal to or greater than the latter for 77.8% of the readings (n = 9). This indicates that cold air drainage frequently occurs. The uppermost thermometer on the east wall (#4; 134 m above study site and 76 m above max/min #3) is consistently cooler than #3, but shows readings equal to or greater than #2 for 44.4% of the readings. Again, cold air drainage is indicated. In addition to the increased differences in elevation, the topographic position of #4 on a less steeply sloping site may decrease the occurrence of cold

Table 9. Deviations in mean monthly temperatures (^oC) and total precipitation (mm) from 1941 - 1970 normals at two weather stations.

Month	Kananaskis (ESC) Temperature	Kananaskis (ESC) Precipitation	Banff Temperature	Banff Precipitation
May 1975	-2.16	-33.78	- .54	-33.27
June 1975	-1.08	-56.39	-1.08	-38.61
July 1975	+6.48	+24.89	+8.82	+26.67
August 1975	-5.22	-23.88	-4.50	+32.00
May 1976	+5.22	-19.30	+4.32	+35.05
June 1976	-5.04	-67.56	-5.40	-13.21
July 1976	- .54	+ 6.35	- .90	- 7.87
August 1976	+2.88	+24.13	+ 1.98	+30.73

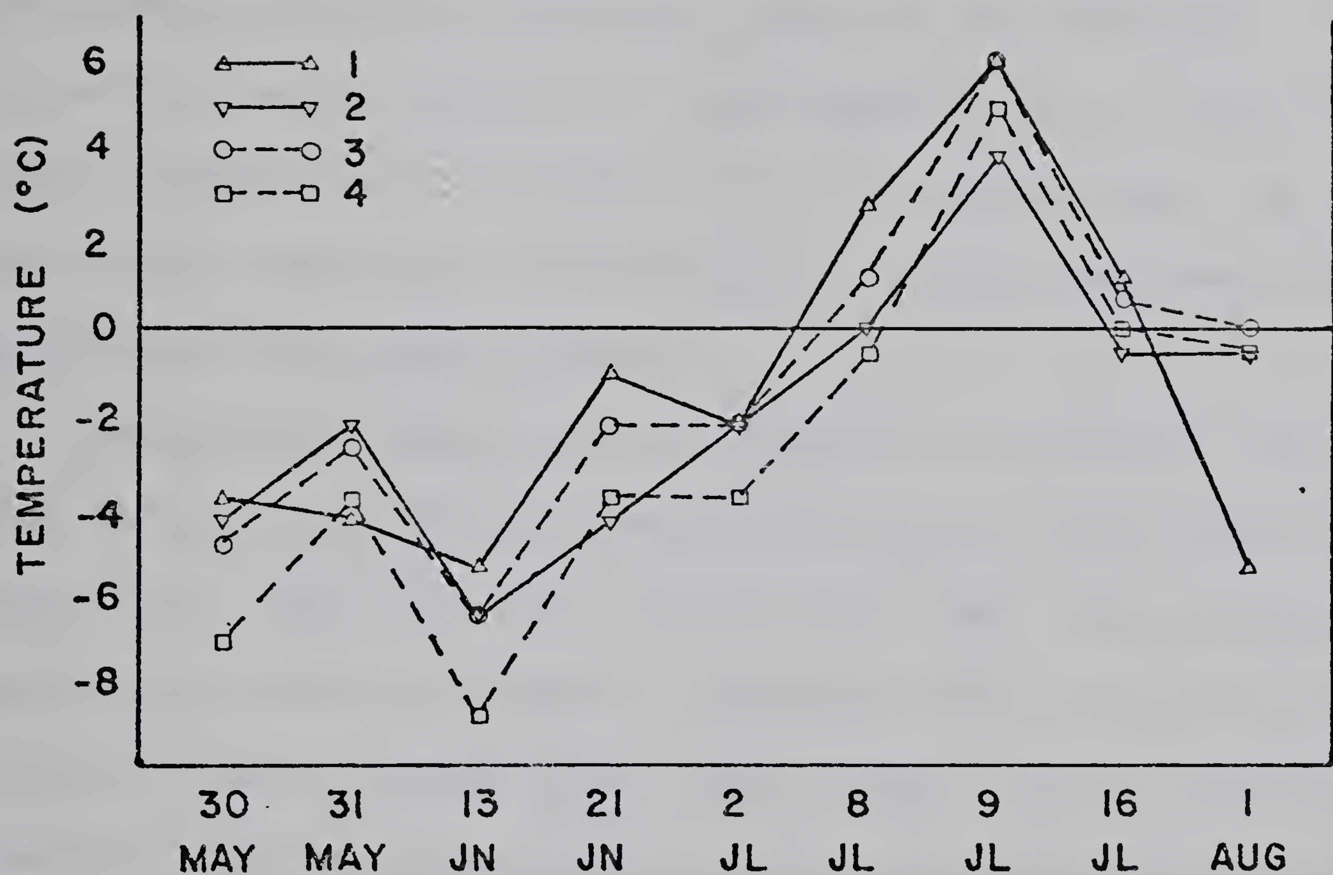


Figure 5. Minimum air temperature (^{O}C) for four maximum minimum thermometers at Wind Creek, 1976. See text for thermometer locations.

air drainage from this site. Data from #1 also indicate the occurrence of cold air drainage, as 77.8% of the readings were greater than or equal to readings on the valley bottom.

Precipitation

Data collected by the Atmospheric Environment Service, Environment Canada, at the Marmot site indicate that both 1975 and 1976 were wetter than average during July and August (based on the period 1963 - 1976) (Table 10). Data collected at a lower elevation (Con 5, Table 10) shows summer precipitation to be quite similar to average values. On an annual basis, much less precipitation fell in these two years, resulting mainly from little winter snowfall.

Precipitation data from weather stations at Kananaskis (ESC) and Banff indicate that 1975 was somewhat drier than average (based on the period 1941 - 1970) (Table 9). During 1976, lower than average summer precipitation fell at Kananaskis, but greater than average amounts fell at Banff. These different trends among stations reflect differences in elevation, local physiography and location, and much care should be exercised in interpreting such comparisons.

Comparative information for the Marmot and Wind Creek sites shows no significant difference in total precipitation over a two month period (July and August) (Table 11). Based on precipitation data from other stations in the region, June would be expected to yield the highest amount of precipitation.

Total precipitation is only one component which interacts to determine the overall water budget of an area. Other factors include soil type, vegetation type and evapotranspiration. One factor important to

Table 10. Precipitation (mm) over a fourteen year period at two stations in the Marmot Creek basin watershed.

	Marmot	Con 5*	
Year	June 30-August 28	Annual	June-August
1963	273	881	412
1964	95	691	161
1965	204	849	348
1966	161	594	192
1967	98	514	134
1968	184	632	206
1969	118	620	220
1970	80	603	225
1971	65	709	178
1972	239	641	165
1973	90	593	178
1974	132	716	141
1975	216 (+63)#	614 (-44)	210 (-3)
1976	188 (+35)	552 (-106)	218 (+5)
$\bar{X}$	153	658	213

* located at 1770 m within the Marmot Creek Basin

\# values in parentheses are deviations from the 1963-1976 average

Table 11. Precipitation (mm) at Marmot and Wind Creek (1976).

Month	Marmot	Wind Creek
July	49.0	86.1
August	138.7	95.0

Table 12. Mean monthly and mean summer wind speeds ($m \cdot sec^{-1}$) (1 = partial month) at Marmot (1975 and 1976) and Wind Creek (1976).

Month	Marmot 1976	Marmot 1976	Wind Creek 1976
May	-	2.36[1]	2.62[1]
June	2.55[1]	1.53	1.59
July	1.00	1.29	-
August	.50	1.23	3.24
Total	1.22	1.39	2.53

evapotranspiration is the amount of wind reaching an area. This component has been measured, and is discussed below.

Wind

Like air temperature, mean wind velocities at the two sites are considerably different. The impression that one gets of the windiness of the Wind Creek cirque is supported by measurements taken during the summer of 1976. Table 12 summarizes mean monthly wind speeds at the two study sites. These data indicate that 1976 was windier than 1975 at the Marmot site, and that the Wind Creek site was 1.58 times more windy than the Marmot site during 1976.

Short term mean wind speeds in Wind Creek were often quite high; the three day mean from 18 August to 21 August was 5.07 m sec^{-1}; the ten day mean from 18 August to 28 August was 4.16 m sec^{-1}.

This difference in mean wind speeds is best interpreted as resulting from the difference in orientation between the two cirques. The north-facing Wind Creek cirque opens onto the very large Bow River Valley, and thus is subject to the often high winds which originate to the west, and travel along the Bow River.

The Marmot cirque faces east into the smaller Kananaskis River Valley. This north - south valley is not subjected to the same air movement patterns as is the Bow Valley. The increased occurrence of chinooks in the Kananaskis Valley may introduce an added element of complexity to this comparison. Winter wind patterns would not necessarily be the same as those described above.

Radiation

Mean incoming shortwave radiation has been summarized for weekly intervals (Figure 6). Except for the week beginning 1 August, radiation at Wind Creek was consistently less than at Marmot during 1976, averaging only 78.4% of the latter. This difference was especially pronounced during the week of 11 July, when Marmot received its maximum energy. Marmot values for 1975 were also consistently lower than for 1976, averaging 72.9% of the latter.

The lower radiation input at Wind Creek is consistent with observations of cloud patterns. Westerly winds often backed up clouds behind the summit ridges of Mount Allan. These clouds often spilled over into the Wind Creek cirque, whereas the Marmot cirque remained cloud-free. In addition, the high cirque walls of Wind Creek shortened the day length by effectively delaying sunrise and advancing sunset.

Vapor Pressure Deficit

Mean values of vapor pressure deficit (VPD) have been calculated for weekly intervals (Table 13). It is evident that Wind Creek had consistently higher deficits than Marmot, and that at Marmot, 1975 deficits were consistently higher than 1976 deficits. The maximum weekly mean deficit at Marmot was 3.13 mb in 1976 and 5.70 mb in 1975. The corresponding maximum at Wind Creek was 4.49 mb. Weekly means based on only noon temperature and relative humidity readings show somewhat higher VPD's, but a similar pattern. In all cases, maximum values occurred during early to mid July. A value of 4.66 mb was calculated for noon readings at Marmot in June 1975, but this was based on only two measurements.

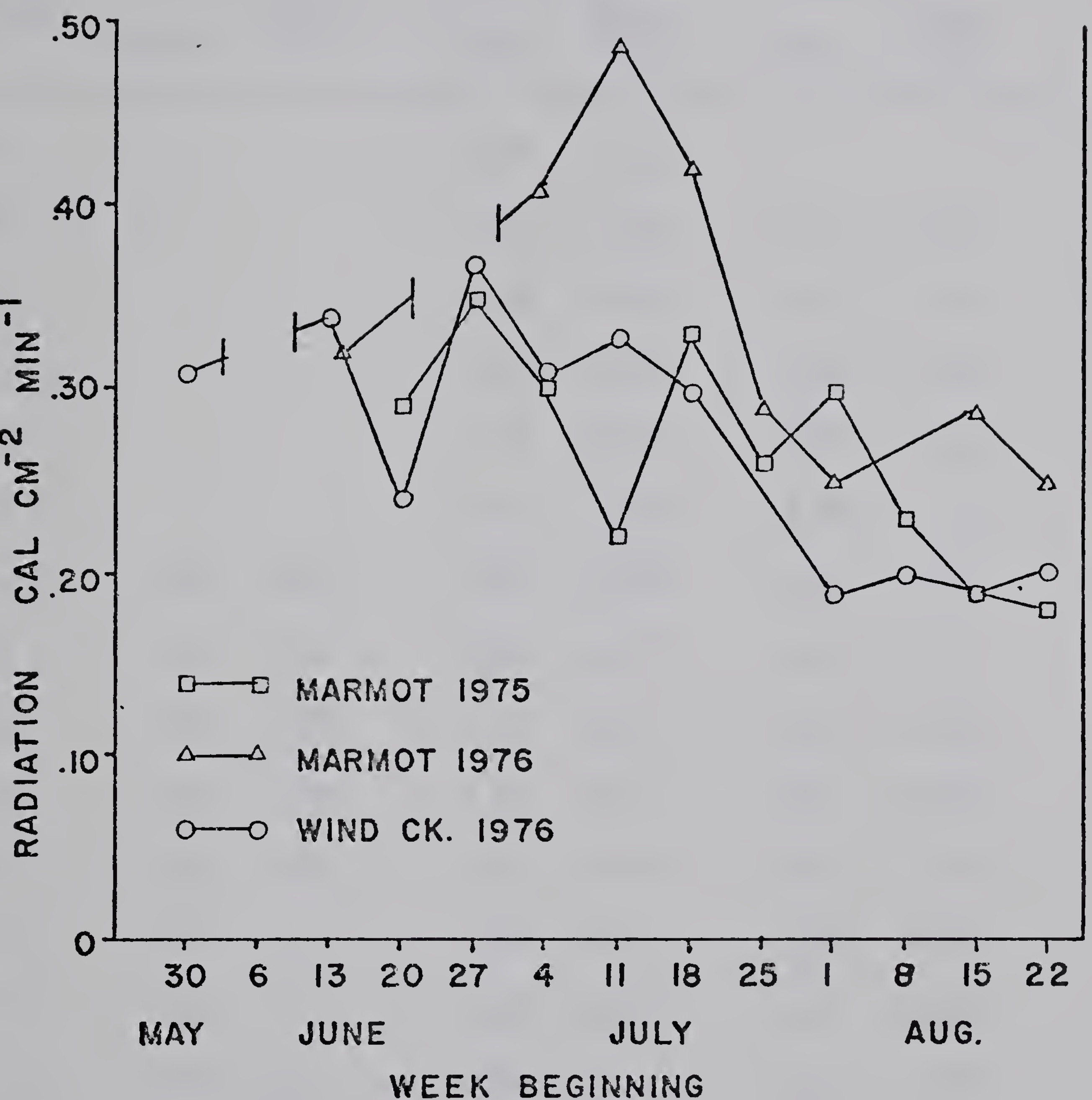


Figure 6. Mean weekly global radiation at Marmot (1975 and 1976) and Wind Creek (1976).

Table 13. Mean weekly vapor pressure deficit (mb) for Marmot (1975 and 1976) and Wind Creek (1976). Values for daily (measurements at 6 hr interval) and noon readings are included.

	Marmot		Marmot		Wind Creek	
	1975		1976		1976	
Week Beginning	Daily	Noon Only	Daily	Noon Only	Daily	Noon Only
May 23			2.14	2.76		
May 30			1.93	2.29	1.21	2.79
June 6			2.23	2.62	1.59	2.87
June 13			2.93	4.66	2.90	2.85
June 20			1.91	2.38	2.26	2.73
June 27			3.13	4.10	4.28	6.52
July 4	5.70	9.45	2.56	2.59	2.67	5.29
July 11	3.13	5.89	2.84	3.01	3.86	5.95
July 18	5.23	7.04	2.80	2.78	4.49	6.52
July 25	3.74	4.45	1.83	3.21	2.61	4.58
August 1	3.99	6.26	1.29	2.79	1.08	2.24
August 8	2.16	3.31	1.67	2.55	1.80	2.99
August 15	1.07	2.11	1.67	2.08	2.57	2.82
August 22	1.78	2.37	2.03	2.31	3.30	3.78

Of the two components of VPD, temperature has already been discussed. Relative humidity will not be discussed independently, as it is less meaningful biologically than vapor pressure deficit. One observation of interest, however is that the amplitude (range) of RH values at Marmot was consistently less than at Wind Creek.

VEGETATION

A total of eight plant communities have been delineated at these two sites, five at Marmot and three at Wind Creek. These communities were subjectively delineated on the basis of the codominant species and plant structure. These communities provide a basis for a number of comparative analyses between the two sites and between these communities and species assemblages on ground squirrel burrow mounds. Similar assemblages of species occur elsewhere in the Front Ranges, but because extensive sampling was not undertaken, their occurrence on a geographic basis cannot be documented here.

Data were placed in a Braun-Blanquet type synthesis table (Mueller-Dombois and Ellenberg 1974) which allowed relationships between quadrats to be more readily observed. This treatment led not only to an understanding of the plant communities, but also aided in understanding the community - environment relationships. With such a foundation, the two sites and their respective plant communities can be compared.

Marmot

The Marmot site was studied in more detail and will be discussed first. This site includes only a small portion of the complex vegetation mosaic which patterns the Marmot cirque. Islands and ribbons of *Abies lasiocarpa* (subalpine fir) and *Picea engelmannii* (Engelmann spruce) cover portions of the cirque floor and sidewalls. At approximately 2225 m, *Larix lyallii* (alpine larch) becomes the dominant tree species, and forms a band of open woodland 50 - 250 m wide between

the fir-spruce forest below and the fir-spruce krummholz and alpine vegetation above. Amidst these forest stands are a variety of meadows ranging from the subalpine types described below to alpine types at higher elevations. Willow scrub (mainly Salix glauca) occurs on the cirque floor and along Middle Fork Creek in wetter areas.

The 1500 m^2 study area is bounded by alpine larch woodland above and willow scrub below. Despite its small size, species richness in this meadow is high, with 102 vascular species representing 71 genera and 31 families. The Compositae is the most important family, with 8 genera and 14 species. The Ranunculaceae is also quite important with 10 species in five genera. Other families with five or more species include Graminae (9), Rosaceae (7), Caryophyllaceae (6), Cruciferae (6), Pinaceae (5) and Scrophulariaceae (5) (see Appendix I for a complete list). Species of lichens, mosses and liverworts totaled 9, 20 and one respectively. The cryptogam estimates are perhaps low, but vascular species estimates are very close to the actual number present.

These observations convey some understanding of the meadow as a total unit, but do not adequately describe the species assemblages or distinct plant communities. Although actual examples of homogeneous plant communities are not common in well-drained subalpine meadows, the individual responses of species to the environmental complex (sensu Billings 1952) do result in relatively similar associations under similar environmental regimes. Such communities have been delineated at Marmot (Figure 7), and are described below.

Figure 7. Location of five plant communities, Marmot: Epilobium-Bromus (E-B); Juniperus-Arctostaphylos (J-A); Snowbank (Sn); Wet forb (Wf); and Mesic grass (Mg).

<u>Juniperus communis - Arctostaphylos uva-ursi</u>

This dwarf shrub community is the most xeric in the meadow and is found in a continuous band at the highest topographic positions. These well-drained sites receive a large amount of solar radiation which causes high soil surface temperatures. Richards (1976, pers. comm.) has recorded temperatures as high as $31^{0}C$ on exposed soil within a nearby larch woodland. These sites also have more surface gravel, more acidic soils and slightly thinner soil horizons than adjacent areas. Decreased winter snow cover results from their increased exposure (Figure 8).

The increased soil temperatures and decreased water availability which results from this combination of factors affects the vegetation in several ways: 1) vascular plant cover is reduced ($\overline{X}$ = 68%); 2) bryophytes are much less important; and 3) the importance of woody species such as <u>Juniperus</u> and <u>Arctostaphylos</u> increases.

<u>Epilobium angustifolium - Bromus pumpellianus</u>

A mesic zone is located on midslope positions below the xeric <u>Juniperus</u> - <u>Arctostaphylos</u> zone. These intermediate positions also receive large amounts of solar radiation due to their south-facing aspect. Soils on these sites are well-drained and have relatively well-developed horizons. Winter snow depths are 2 - 4 x those on <u>Juniperus</u> - <u>Arctostaphylos</u> sites (Figure 8).

This combination of factors results in the presence of a relatively lush assemblage of herbaceous species (n = 46) with nearly complete vascular cover ($\overline{X}$ = 91%). The dominant taxa on these sites

Figure 8. Snow depths (cm) at selected sites, 23 February, 1976, Marmot.

are Epilobium angustifolium, Bromus pumpellianus, Achillea millefolium, Hedysarum sulphurescens and Poa spp.

Wet forb

Topographic lows support a very distinctive wet forb community in which Epilobium angustifolium, Oxyria digyna, Senecio triangularis and Erigeron peregrinus are codominant. These areas had standing water which persisted until late June in 1975 and early June in 1976. Winter snow depths on this site are exceeded only by the Snowbank community (Figure 8). This results in a unique assemblage of vascular plants and a nearly continuous bryophyte layer of Bryum pseudotriquetrum. Although species richness in this community is low (n = 13), total vascular cover is extremely high ($\overline{X}$ = 97.3%). This lush green community is in sharp contrast to the drab ridgetop Juniperus - Arctostaphylos community.

Snowbank

A snowbank site dominated by Solidago multiradiata, Arenaria capillaris, Potentilla diversifolia, Vaccinium scoparium and several graminoids is found at the western end of the meadow in a southeast-facing concavity. In 1975, snowmelt was complete by early June in all areas except the snowbank site, which did not melt out until mid-June. Corresponding dates for 1976 were mid-June for the snowbank site and late May for the rest of the meadow. February snow depths were .9 - 1.2 m on this site. The presence of late-lying snow modifies the environment in several ways. The effects of shortened growing season, increased water availability and decreased soil temperature are well known and have been documented by Billings and Bliss (1959) and

Canaday and Fonda (1974). Soils also reflect this modified environment. Thickness of the B horizon was 2 - 4 x that of B horizons from other sections of the meadow.

Mesic grass

The mesic grass community occurs on level ground in the eastern portion of the meadow. It occurs adjacent the wet forb community and is influenced by this proximate source of water. Here the moisture regime is intermediate between that of the Wet forb and the mesic Epilobium - Bromus communities. This community is characterized by the decreased dominance of Epilobium, increased dominance of graminoids and the presence of species such as Astragalus alpinus and Senecio lugens which are more common at the Wind Creek site. The presence of this community may be accounted for by the increased soil moisture, decreased soil temperatures and the level position, which receives less solar radiation than the adjacent south-facing slopes.

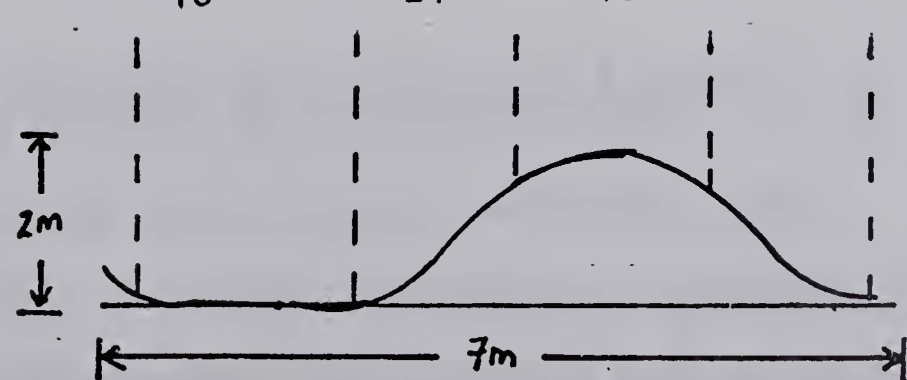
The pattern of plant communities described above can best be explained on the basis of a mesotopographic gradient (sensu Billings 1973). Table 14 summarizes data collected over such a gradient. Although this table is based on a particular transect, it is representative of similar transects throughout the meadow. Certain trends are immediately evident. Species richness is lowest in the hydric, depressional areas (13), and highest in midslope positions (24 and 19). Mean vascular plant cover is lowest on the ridgetop (90%) and highest in the depressions (99%). Other patterns can be observed by examining the Importance Values (see below) of particular species. For example, Epilobium angustifolium and Erigeron peregrinus occur at all four sites

Table 14 Importance Values for taxa over a mesotopographic gradient at Marmot. Quadrat numbers are given in parentheses.

Species	Depression (6)	Midslope (11)	Ridgetop (8)	Midslope (12)
Epilobium angustifolium	39.41	10.40	20.98	26.14
Oxyria digyna	30.83	-	-	-
Senecio triangularis	29.80	-	-	-
Erigeron peregrinus	26.59	1.72	2.96	2.44
Stellaria spp.	15.26	-	-	-
Graminoids	14.81	39.81	19.74	40.81
Achillea millefolium	14.23	17.65	11.05	18.41
Valeriana sitchensis	9.45	-	-	-
Delphinium glaucum	7.99	-	-	-
Potentilla diversifolia	3.99	14.76	7.63	13.45
Bromus pumpellianus	2.84	16.63	9.78	19.83
Anemone spp.	2.39	-	-	-
Epilobium glandulosum	2.39	-	-	-
Hedysarum sulphurescens	-	23.89	2.83	21.94
Penstemon procerus	-	16.63	4.07	15.18
Solidago multiradiata	-	12.81	6.11	6.77
Fragaria virginiana	-	11.79	12.57	19.62
Cerastium arvense	-	6.34	1.78	0.99
Campanula rotundifolia	-	5.16	4.96	2.10
Myosotis alpestris	-	4.47	-	1.06
Rumex alpestris	-	2.51	-	3.88

Table 14 continued

Species	Depression (6)	Midslope (11)	Ridgetop (8)	Midslope (12)
Rumex alpestris	-	2.51	-	3.88
Gentiana amarella	-	2.43	-	-
Equisetum pratense	-	2.26	-	-
Allium cernuum	-	2.19	-	-
Arctostaphylos uva-ursi	-	1.72	28.31	-
Antennaria alpina	-	1.71	2.57	-
Botrychium spp.	-	1.65	-	0.93
Astragalus alpinus	-	0.93	-	-
Arenaria capillaris	-	0.86	1.65	-
Veronica wormskjoldii	-	0.86	-	-
Polygonum viviparum	-	0.79	-	-
Juniperus communis	-	-	57.19	-
Sedum lanceolatum	-	-	3.54	1.19
Phacelia sericea	-	-	2.30	-
Vaccinium scoparium	-	-	-	1.94
Eriogonum subalpinum	-	-	-	1.87
Agoseris aurantiaca	-	-	-	1.47
mean vascular cover	99.0	92.4	89.8	97.9
species richness	13	24	18	19



but are much more important in the depressional area. Bromus pumpellianus shows an opposite trend, being more important on well-drained sites, and less so in depressional areas. Many taxa occur on all three well-drained sites. Of these, graminoids, Achillea millefolium, Potentilla diversifolia, Bromus pumpellianus, Hedysarum sulphurescens and Penstemon procerus are much more important on midslope versus ridgetop positions. Conversely Arctostaphylos uva-ursi and Juniperus communis are very important on ridgetop positions, and unimportant or absent on midslope sites.

In summary, five plant communities were recognized at Marmot. Their spatial distribution is controlled by topographic position and drainage patterns (Figure 7). They form a dramatic gradient from wet forb to mesic midslope to xeric ridgetop communities within a very short distance. Species distributions range from ubiquitous (e.g. Epilobium angustifolium and Bromus pumpellianus) to highly restricted (e.g. Oxyria digyna, Juniperus communis and J. horizontalis). Table 15 is based on the Importance Values of the common taxa and compares these five communities. Importance Values (IV) were calculated as follows:

$$\text{IV} = \text{Relative Cover} + \text{Relative Frequency}$$

where

$$\text{Relative Cover} = \frac{\text{Mean cover of species A}}{\text{Sum of mean cover values of all species present}} \times 100$$

and

$$\text{Relative Frequency} = \frac{\text{Number of quadrats in which Species A occurs}}{\text{Sum of this value for all species present}} \times 100$$

Table 15 provides an understanding of species performance under different environmental regimes. For instance, Epilobium angustifolium, with an IV of 19.84 for the entire meadow, has a range of 5.85 to 39.41

Table 15. Importance Values of selected taxa in five communities, Marmot site. Only taxa with Importance Values > 5.00 in atleast one community are included.

Species	Epilobium-Bromus	Juniperus-Arctostaphylos	Wet Forb	Snowbank	Mesic Grass	Total Meadow
Graminoids	29.02	14.98	14.81	16.65	31.48	23.27
Epilobium angustifolium	26.62	11.56	39.41	14.21	5.85	19.84
Juniperus communis	-	48.74	-	3.29	-	16.39
Achillea millefolium	17.21	9.99	14.23	11.96	20.86	14.47
Potentilla diversifolia	14.04	9.91	3.99	16.49	16.00	12.74
Bromus pumpellianus	17.62	7.20	2.84	6.32	19.13	12.57
Solidago multiradiata	9.36	9.36	-	17.90	24.55	11.30
Hedysarum sulphurescens	16.40	3.10	-	1.43	15.19	9.86
Erigeron peregrinus	12.39	1.38	26.59	5.80	4.29	7.87
Penstemon procerus	10.22	5.41	-	1.21	3.45	6.83
Fragaria virginiana	10.43	2.59	-	-	3.38	6.07
Arctostaphylos uva-ursi	.23	15.03	-	-	-	5.05
Vaccinium scoparium	1.45	7.65	-	16.27	-	4.56
Eriogonum subalpinum	4.39	5.50	-	7.56	-	4.28
Saxifraga bronchialis	-	7.96	-	1.29	-	2.81

Table 15. (continued)

	Epilobium-Bromus	Juniperus-Arctostaphylos	Wet Forb	Snowbank	Mesic Grass	Total Meadow
Valeriana sitchensis	1.59	-	9.45	5.72	-	1.54
Oxyria digyna	-	-	30.83	-	-	.97
Senecio triangularis	-	-	29.80	-	-	1.07
Delphinium glaucum	-	-	7.99	-	-	.27
Stellaria spp.	.34	.13	15.26	-	4.27	.94
Antennaria lanata	1.28	3.28	-	11.41	-	2.69
Arenaria capillaris	2.20	4.46	-	16.56	-	3.89
Selaginella densa	.68	3.44	-	9.77	-	2.42
Sibbaldia procumbens	.53	1.71	-	9.81	-	1.71
Pedicularis contorta	.62	.67	-	7.94	-	1.24
Myosotis alpestris	2.87	1.00	-	-	7.44	2.24
Astragalus alpinus	1.22	-	-	-	7.04	1.11
Equisetum pratense	1.48	-	-	-	5.85	1.17
Gallium boreale	1.60	.29	-	-	11.06	1.74
Juniperus horizontalis	.23	7.79	-	-	-	2.58
Total plant cover (%)	93.1	70.5	99.0	69.0	97.4	81.41
Total vascular cover (%)	92.4	68.4	97.3	66.3	96.3	79.61

when calculated for each community. Achillea millefolium shows much less variance in its values: 14.47 for the meadow and a range of 9.99 - 20.86. More restricted species such as Juniperus communis and Arctostaphylos uva-ursi also have a wide range in values. Meadow values and ranges for these two species were 16.39 (0 to 48.74), and 5.05 (0 to 15.03) respectively.

Wind Creek

As mentioned earlier, the Wind Creek cirque faces north into the Bow River Valley whereas the Marmot cirque faces east into the Kananaskis River Valley. This difference in aspect causes significant changes in the environment, and hence the vegetation. The floor of the Wind Creek cirque is only lightly forested by upright trees and krummholz of subalpine fir. Engelmann spruce and alpine larch are less important. On the sidewalls is an inverted timberline of subalpine fir and Engelmann spruce. Most common on the cirque floor are herbaceous meadows, dwarf heath shrub and willow scrub communities. This patterning is probably the result of a combination of cold air drainage, late-lying snow on the cirque floor, frequent strong winds and destructive winter avalanches.

The Wind Creek study site is situated on level ground surrounding a small, permanent pond (Figure 9). This herbaceous meadow, though larger than the Marmot site, is less rich floristically. The 73 vascular taxa present are distributed among 51 genera in 23 families. The most important family is Compositae with 11 species in seven genera. Other important families include Caryophyllaceae, Ranunculaceae, Cruciferae and Scrophularíaceae, all with five species.

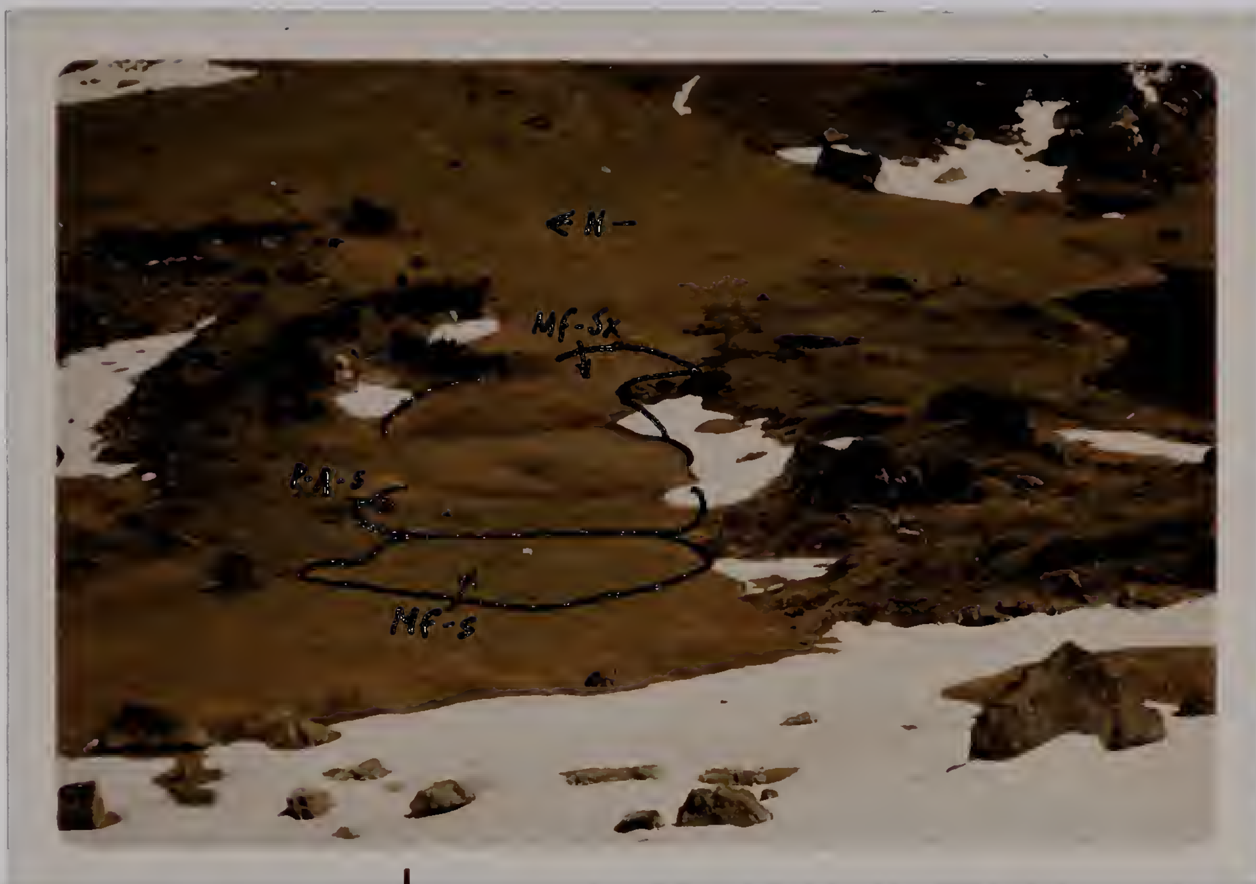


Figure 9. Location of three plant communities, Wind Creek: Potentilla-Achillea-sedge (P-A-s); Mixed forb-sedge (Mf-s); and Mixed forb-Salix (Mf-Sx).

Lichen, moss and liverwort species collected or observed totaled seven, 9 and 1 respectively.

This site can also be separated into areas of increased homogeneity, or areas which represent distinct plant communities. Of the several plant communities present, three were considered most significant on the basis of either their areal extent or their intensity of use by ground squirrels. All three occurred on level to gently sloping ground surrounding the central pond of the study area on terraces which were presumably formed by the downslope movement of soil.

Potentilla diversifolia - Achillea millefolium - sedge

This community is found to the west of the pond on the two lowest terraces (Figure 9) and has a mean vascular plant cover of 87.1% with 31 taxa present. Table 16 gives Importance Values for the taxa in all three Wind Creek communities. Of particular importance are Potentilla diversifolia (IV = 25.26), Achillea millefolium (22.49) and Astragalus alpinus (15.14). These herbs are found intermixed with the two dominant sedges, Carex phaeocephela and Carex sp.

Mixed forb - sedge

This community occurs further west and above the Potentilla - Achillea - sedge community on the third and highest terrace. It differs from the above community by the increased importance of Solidago multiradiata (19.56 vs. 6.03), Senecio lugens (12.41 vs. 3.28), Stellaria sp. (10.67 vs. 5.36) and Carex phaeocephala (17.35 vs. 6.72). Erigeron peregrinus, Sibbaldia procumbens and Salix drummondiana

Table 16. Importance Values of taxa in three communities, Wind Creek study site.

Taxa	Communities		
	Potentilla-Achillea-sedge	Mixed forb -sedge	Mixed forb -Salix nivalis
Graminoids	26.64	20.09	22.12
Potentilla diversifolia	25.26	22.97	24.93
Achillea millefolium	22.49	23.31	18.48
Astragalus alpinus	15.14	17.85	18.87
Myosotis alpestris	9.84	11.70	3.19
Erigeron peregrinus	8.56	-	-
Salix drummondiana	8.43	-	-
Cerastium arvense	8.17	11.03	7.52
Sibbaldia procumbens	8.16	-	7.93
Rumex alpestris	7.09	6.95	6.70
Carex phaeocephala	6.72	17.35	6.77
Sedum lanceolatum	6.65	3.06	1.76
Solidago multiradiata	6.03	19.56	12.10
Stellaria sp.	5.36	10.67	1.76
Penstemon procerus	4.96	4.58	4.86
Agoseris glauca	3.82	-	-
Veronica wormskjoldii	3.74	1.37	1.93
Senecio lugens	3.28	12.41	6.44
Polygonum viviparum	2.90	2.88	5.28
Arenaria capillaris	2.22	-	10.17
Hedysarum sulphurescens	2.14	-	-
Gentiana amarella	2.14	-	-

Table 16. (continued)

	Communities		
	Potentilla-Achillea-sedge	Mixed forb -sedge	Mixed forb -*Salix nivalis*
Elymus innovatus	2.06	-	-
Androsace septentrionalis	1.52	3.23	1.45
Ranunculus eschscholtzii	1.45	1.69	1.60
Salix nivalis	1.60	2.04	13.21
Stellaria spp.	1.22	-	-
Phleum alpinum	.83	-	-
Polemonium pulcherrimum	.83	-	-
Botrychium spp.	.69	-	-
Salix arctica	-	2.20	-
Aquilegia flavescens	-	1.86	-
Besseya wyomingensis	-	1.69	-
Smelowskia calycina	-	1.52	-
Salix barrattiana	-	-	6.39
Silene acaulis	-	-	6.39
Antennaria lanata	-	-	6.00
Antennaria umbrinella	-	-	2.59
Anemone spp.	-	-	1.60
$\bar{X}$ vascular cover	87.08	95.33	88.67
$\bar{X}$ bryophyte cover	25.77	6.50	6.50
$\bar{X}$ lichen cover	4.15	2.50	8.83

are absent, yet all are important in the previous type. The Mixed forb-sedge community has 22 taxa, and a mean vascular cover of 95%, a mean bryophyte cover of 7%, and a mean lichen cover of 3%.

Mixed forb - Salix nivalis

This community occurs on a terrace to the east of the pond and differs from the above two by the increased importance of Arenaria cappilaris (IV = 10.17) and Salix nivalis (13.21). Other dominants tend to be similar. This community contains 24 taxa, has a mean vascular cover of 89%, a mean bryophyte cover of 7% and a mean lichen cover of 9%.

In summary, three plant communities have been described from the Wind Creek study site. All three occur on terraces, on level to gently sloping ground (Figure 9). They are more similar structurally and floristically than are the five described from Marmot. This increased similarity is a direct result of decreased habitat variability.

Comparison of Marmot and Wind Creek

The above discussion provides a basis for understanding the characteristics and patterning of plant communities within each site. It is now desirable to compare these two sites in an attempt to relate some of the dissimilarities in plant communities to differences in the biotic and abiotic environment. To this end, quantitative values have been calculated which express the degree of similarity between any two communities. This allows similarity matrices to be constructed which compare all communities.

Table 17 compares communities on the basis of the presence and absence of vascular species. These values are calculated as follows:

$$IS_s = \frac{2C}{A + B} \times 100 \qquad \text{(Sørensen 1948)}$$

where C = the number of species common to the two communities, A = the number of species in community A and B = the number of species in community B.

Table 18 compares communities on the basis of species Importance Values. These values are calculated as follows:

$$IS_{mo} = \frac{2\ Mw}{MA + MB} \times 100 \qquad \text{(Motyka et al. 1950)}$$

where Mw = the sum of smaller Importance Values of the species common to two communities, MA = the sum of IV's of all species in community A and MB = the sum of IV's of all species in community B. Mueller-Dombois and Ellenberg (1974) provide a good discussion of the derivation and use of such indices.

The examination of similarity values provides some insight into the floristic relationships which exist between communities. For example, the Epilobium - Bromus community of Marmot is quite similar to the snowbank community based on species presence-absence (Index of Similarity (IS) = 63.16), but is dissimilar when compared on the basis of Importance Values (IS = 25.03). Thus, species in common are important at only one of the sites. Similarly, the Epilobium - Bromus community is very similar to the Juniperus - Arctostaphylos community based on presence-absence (IS = 73.56) but relatively dissimilar based on Importance Values (47.92).

With between-site comparisons, it is evident that the two mesic Marmot communities most closely resemble the Wind Creek communities.

Table 17. A similarity matrix based on presence-absence of species. See text for details.

		Total	Epi-Brom	Jun-Arcto	Wet Forb	Snowbank	Mesic Gr.	Total	Pot-Ach	Forb-Sedge	Forb-Salix
		MARMOT						WIND CREEK			
Total Meadow	MARMOT	-	81.42	75.93	32.50	61.86	54.35	48.74	43.30	33.71	41.76
Epilobium-Bromus	MARMOT		-	73.56	30.51	63.16	61.97	53.06	52.63	41.18	48.57
Juniperus-Arctostaphylos	MARMOT			-	29.63	70.42	51.52	43.01	42.25	28.57	40.00
Wet Forb	MARMOT				-	32.56	36.84	18.46	18.60	17.14	21.62
Snowbank	MARMOT					-	40.00	41.46	43.33	26.92	37.04
Mesic Grass	MARMOT						-	41.56	47.27	42.55	40.82
Total Meadow	WIND CREEK							-	73.17	59.46	63.16
Potentilla-Achillea-Sedge	WIND CREEK								-	69.23	74.07
Mixed Forb-Sedge	WIND CREEK									-	73.91
Mixed Forb-_Salix_	WIND CREEK										-

Table 18. A similarity matrix based on Importance Values. See text for details.

		Total	Epi-Brom	Jun-Arcto	Wet Forb	Snowbank	Mesic Gr.	Total	Pot-Ach	Forb-Sedge	Forb-Salix
				MARMOT					WIND CREEK		
Total Meadow	MARMOT	-	76.60	67.54	35.94	58.38	57.00	46.60	43.15	37.98	21.13
Epilobium-_Bromus_	MARMOT		-	47.92	38.47	25.03	66.13	48.87	48.46	42.30	44.56
Juniperus-_Arctostaphylos_	MARMOT			-	22.84	52.07	36.14	34.91	30.75	27.48	32.18
Wet Forb	MARMOT				-	29.67	25.14	19.51	20.80	16.52	17.31
Snowbank	MARMOT					-	41.88	39.76	37.45	33.82	44.06
Mesic Grass	MARMOT						-	51.74	53.23	56.94	46.85
Total Meadow	WIND CREEK							-	75.10	69.39	76.08
Potentilla-_Achillea_-Sedge	WIND CREEK								-	75.03	70.99
Mixed Forb-Sedge	WIND CREEK									-	69.04
Mixed Forb-_Salix_	WIND CREEK										-

Based on presence-absence, the Epilobium - Bromus community is most similar to the three Wind Creek communities ($\overline{X}$ = 47.46). Based on Importance Values, the Mesic grass community is most similar ($\overline{X}$ = 52.34). This trend reflects the similarities in the moisture regimes of these sites. As expected, some of the highest values resulted from comparisons between the three Wind Creek sites ($\overline{X}$ = 72.40 based on presence-absence; $\overline{X}$ = 71.69 based on Importance Values).

These IS matrices reflect the importance of the abiotic environment on vegetation. Communities at similar points along a topography - moisture continuum show the highest IS values. This is reflected in the comparisons discussed above. The wide range of within-site IS values at Marmot reflects the more varied physical environment which occurs there. Overall, Table 18 probably best represents the ecological relationships between communities as it incorporates cover and frequency values of taxa present.

PLANT PRODUCTION

Plant production data indicate that standing crop increases quite rapidly, and nearly linearly, for a period of approximately ten weeks (Table 19), reaching a maximum during late July or early August. Only the *Epilobium-Bromus* community at Marmot showed a strong divergence from this trend, as standing crop there continued increasing until August 24th. Marmot values from 1975 reached a maximum of 229.8 g dry wt$\cdot$m^{-2} within exclosures and 277.3 g dry wt$\cdot$m^{-2} outside of exclosures. In 1976, of the four communities which were sampled standing crop was highest in the *Epilobium-Bromus* community (maximum = 238.3 g dry wt$\cdot$m^{-2}). Maximum standing crop in the snowbank (Marmot), Mixed forb-sedge (Wind Creek) and Mixed forb-*Salix nivalis* (Wind Creek) communities was 125.4, 155.8 and 112.2 g dry wt$\cdot$m^{-2} respectively.

Although standing crop in the *Epilobium-Bromus* community was significantly higher than in the other three communities, aboveground net primary productivity (rate change of standing crop) was actually quite similar. Table 20 shows net primary productivity for the four communities during the "phase of increase" (until the third sampling) period) and the "leveling off phase" (between the third and fourth sampling periods). Rates of production for these communities were relatively similar during the increase phase, with a range of 2.00 to 3.12 g dry wt m^{-2} day^{-1}. Rates during the second phase showed more variability: negative rates of increase occurred in the Snowbank community (-0.21 g dry wt m^{-2} day^{-1}) and the Mixed forb-sedge community (-1.39 g dry wt m^{-2} day^{-1}); the Mixed forb-*Salix nivalis* community remained constant (0.04 g dry wt m^{-2} day^{-1}); and the *Epilobium* - *Bro-*

Table 19. Standing crop (g dry wt m^{-2}) and standard errors within and outside of exclosures (1975) and in two plant communities at each site (1976).

1975

Condition	12 June	27 June	10 July	3 August	27 August
Within Exclosure	65.0±10.2	91.5±9.6	147.5±16.5	229.8±40.0	215±9.0
Outside Exclosure	51.4±6.9	102.0±12.6	186.9±31.7	277.3±45.4	261.8±46.3

1976

Community	9 June	5-6 July	25 July	24 August
Snowbank	7.5±2.5	91.7±10.3	126.7±14.5	120.3±3.0
Epilobium -Bromus	67.5±2.5	153±12.4	206.7±18.7	240.7±21.9
	31 May	2 July	31 July	18 August
Mixed Forb -Sedge	6.0±1.0	76.3±14.8	157.3±16.0	132.0±25.0
Mixed Forb -*Salix*		54.0±11.4	112.7±14.8	113.3±8.0

Table 20 Net primary production (g dry wt m^{-2} day^{-1}) in four plant communities over two time periods.

Site - community	Increase Phase	Leveling Phase
Marmot		
Snowbank	2.68	-0.21
Bromus-*Epilobium*	3.12	1.12
Wind Creek		
Mixed forb-sedge	2.46	-1.39
Mixed forb-*Salix nivalis*	2.00	.04

mus community increased (1.12 g dry wt m^{-2} day^{-1}). This variability reflects differences in the phenology of the species occurring in these four communities. The graminoids were the source of this increase in the Epilobium - Bromus community during the second phase, increasing from 81.84 to 116.16 g dry wt m^{-2}. In contrast, the forbs remained constant (122.76 to 122.10 g dry wt m^{-2}) during this same period. The high maximum standing crop for this community results both from the increased rate of production and the higher initial standing crop caused by the overwintering of green tissue in grasses and sedges.

PHENOLOGY

Periodic observations of phenologic development of several plant species within permanent plots allowed a comparison of development between different plant communities within sites, and between sites. Two of these 1.5 X 1.5 m plots were monitored at Wind Creek, one in the Mixed forb-sedge community and one in the Mixed forb-*Salix nivalis* community. At Marmot, three plots were used, one in the Snowbank community, one in the *Juniperus-Arctostaphylos* community and one in the *Epilobium-Bromus* community. Figures 10 and 11 graphically depict three stages of plant development in three of these five plots: vegetative growth, flowering and fruiting. These figures provide a means of visualizing the spacing of flowering time among species at these sites.

Data from Wind Creek indicate two time periods during which a flush of flowering occurred (Figure 10). This breakdown results partly from initiation of observations on 8 July. Earlier observation would no doubt have provided a refinement of these interpretations. The first group of species was already flowering on 8 July. This "early group" consisted of several species, with only *Carex phaeocephela* and *Potentilla diversifolia* common to the two plots. *Draba aurea*, which was flowering in plot 1 (Mixed forb-sedge community), was already fruiting in plot 2 (Mixed forb-*Salix nivalis* community).

A later group of species commenced flowering during mid to late July, and these were first recorded on 31 July. Several were common to the two plots.

In general, species in plot 1 seemed to be somewhat earlier in

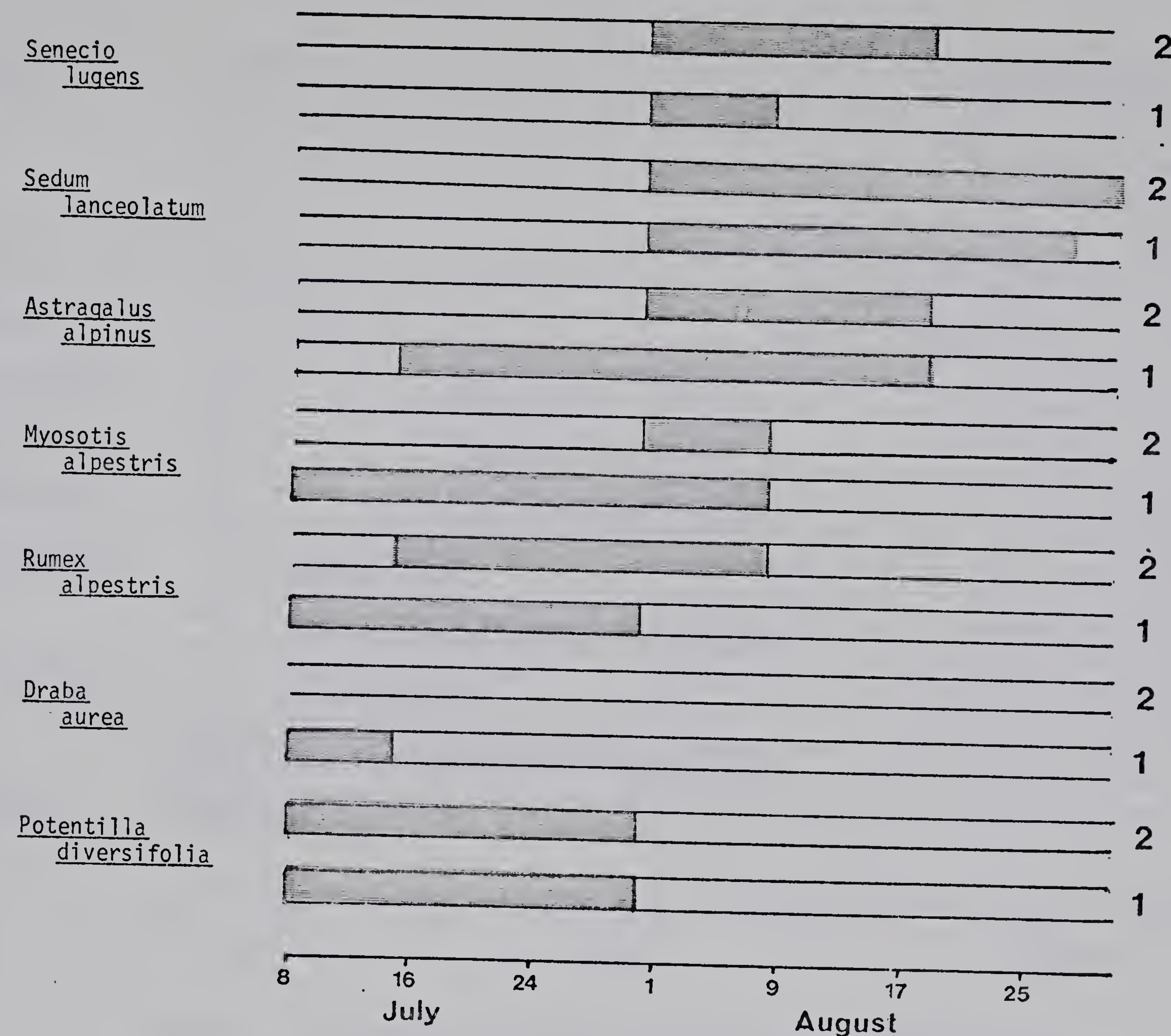


Figure 10. Phenology of selected species in the Mixed forb-sedge (1) and Mixed forb-*Salix nivalis* (2) communities, Wind Creek, 1976. [ ] = in flower.

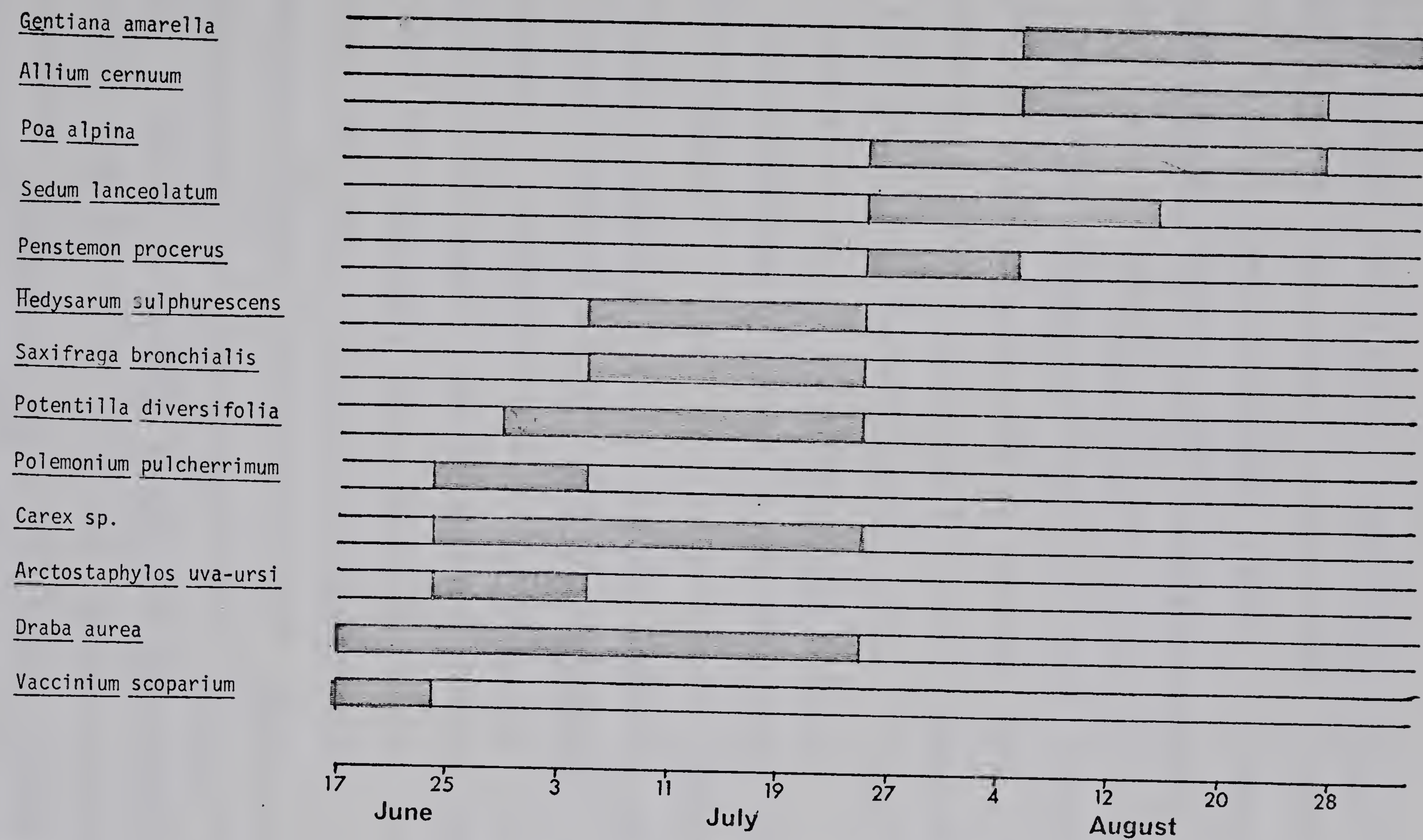


Figure 11. Phenology of selected species in the *Juniperus-Arctostaphylos* community, Marmot, 1976. [shaded box] = in flower.

their development than in plot 2. Although Senecio lugens and Sedum lanceolatum were first recorded in flower on the same date in the two plots, fruiting occurred more quickly in plot 1. In addition, Astragalus alpinus, Rumex alpestris and Myosotis alpestris flowered earlier in plot 1. Only Draba aurea flowered earlier in plot 2.

Observations in Marmot were begun much earlier (3 June), and no species were flowering within plots at that time. This, in addition to the increased number of observations (12, vs. 6 at Wind Creek) allowed for a much finer resolution of phenologic patterns. Figure 11 shows this pattern for the Juniperus-Arctostaphylos community.

The earliest group of species includes those which commenced flowering between 4 - 17 June. This group included Sibbaldia procumbens and Claytonia lanceolata in plot 1 (Snowbank community), Draba aurea and Vaccinium scoparium in plot 2 (Juniperus-Arctostaphylos community) and Potentilla diversifolia in plot 3 (Epilobium-Bromus community). A relatively large number of species commenced flowering between 17 June and 5 July, some being found in more than one plot. Another relatively large number of species first flowered between 5 - 24 July. A late group of species flowered after 24 July: Campanula rotundifolia, Erigeron peregrinus and Allium cernuum in plot 1; Allium and Gentiana amarella in plot 2; and Penstemon procerus and Bromus pumpellianus in 3. Finally, some species never did flower: Epilobium angustifolium in all three plots; Bromus pumpellianus and Pedicularis contorta in plot 1; Achillea millefolium and Myosotis alpestris in plot 2; and Achillea and Arctostaphylos uva-ursi in plot 3.

At Marmot, plot 2 appears to be more advanced than plot 3. Hedysarum sulphurescens and Penstemon procerus both flowered earlier in the former. Also, Poa sp. flowered in the former, but not the latter.

Although the above groupings indicate similar initiation dates for flowering, this does not imply equal periods of time in flower. For instance, Sibbaldia procumbens, Antennaria lanata and Valeriana sitchensis were the first three to flower in plot 1 at Marmot. But whereas Sibbaldia was in flower for only 18 days, Antennaria and Valeriana were in flower for 47 and 42 days respectively. It should be noted that these time-spans do not apply to individual plants, but to the species as a whole. Campanula rotundifolia and Erigeron peregrinus are also likely to have a very short flowering period, as they did not commence flowering until August 27. It is also obvious that many species are marginally able to flower in these habitats. Although Epilobium angustifolium had formed several flower buds by the first few days of September, flowering was not completed. A very small percentage (much less than ·1%) of Epilobium plants at Marmot did flower successfully, but the vast majority finished the growing season still in bud, or in the vegetative stage.

Qualitative observations over two growing seasons indicate that at any time during the summer, particular species can be found in flower. The earliest species flower as the snowline retreats, and are setting seed as later-flowering species are forming and expanding flower buds. This overlapping sequence continues until late summer, when either snowfall or low temperatures, or both, end the growing season. But despite this partitioning of time between species, peak flowering does occur in early to mid July, at which time these meadows become

exceptionally colorful.

GROUND SQUIRREL POPULATIONS

Although Columbian ground squirrels were the most obvious residents of these sites, populations were quite low during the summer of 1975. Only three adults occupied the Marmot site in 1975, and no young were seen above ground. Circumstantial evidence suggests that one of these adults was a female which did produce a litter. During late June and early July, this squirrel spent little time above ground, and it tended to be more vocal and more aggressive when it did emerge. Mattedfur on its stomach also suggested that it was a lactating female with a litter. During the following summer, adult numbers increased to five, and one litter of three was successfully weaned.

These figures indicate that squirrel population size can change dramatically from year to year. The relatively small population of 1975 may be attributable to high winter mortality. Boag (1976 pers. comm.) found low survival for that winter at his study site 50 km to the southeast. The large number of burrows at Marmot (n = 104) suggests either that population size can be much higher than observed during these two years, or that this site has been occupied for a long period of time.

The Wind Creek population (n = 10) was larger than the Marmot population in 1976, with a density of 0.002 squirrels per m^2 (vs. 0.005 m^{-2} at Marmot). Burrows at Wind Creek totalled 116 (0.02 m^{-2}) versus 104 (0.07 m^{-2}) at Marmot.

Utilization of plant communities by squirrels is neither random nor equally distributed. The Wet forb and Mesic grass communities at

Marmot are too wet for burrowing, but squirrels do feed in these areas. Burrows are concentrated in the Epilobium - Bromus and Juniperus - Arctostaphylos communities, with a few in the Snowbank community, and most feeding takes place in the former. At Wind Creek, burrows tend to occur either in areas of increased topographic variability or in association with large surface boulders. Since more of these areas are in the Potentilla - Achillea - sedge and Mixed forb - sedge communities than in the Mixed forb - Salix community, burrows are concentrated in the former two. This also increases the amount of feeding which takes place in these two communities.

DISCUSSION

These comparative data provide the basis for relating plant production, phenology, plant communities and soils to observed differences in physical features and microclimate. To a lesser degree, the presence and role of Columbian ground squirrels can be related to these same factors.

Significant microclimatic differences occur between the sites. Wind Creek is windier and cooler than Marmot. This results primarily from the north aspect of the former versus the east aspect of the latter, as movement of wind eastward along the Bow Valley is funnelled into Wind Creek. This airflow pattern may also partially explain temperature differences, but the location and aspect of the sites within the two cirques is more important in this regard. The Marmot site is on a south-facing slope, which results in relatively high amounts of solar radiation and resultant high soil and near-surface air temperatures. The Wind Creek site is on level ground, which reduces the amount of solar radiation received. The presence of very high cirque sidewalls to the east and west of the site also reduces radiation received by effectively shortening daylength.

The combined effects of soil texture and structure, wind, precipitation and radiation combine to determine soil moisture available to plants. Since precipitation at the sites was essentially equal, this factor can be ignored. The increased radiation load at Marmot increases potential evapotranspiration from the soil. This is especially important on exposed gravelly soils which do not hold capillary water very tightly. In contrast, the greater wind speeds at

Wind Creek increases potential evapotranspiration at that site. Table 13 indicates that Wind Creek had consistentlygreater vapor pressure deficits (VPD) than Marmot. In addition to the combination of factors mentioned above, the location of the hygrothermographs was also important in determining the VPD. The Wind Creek hygrothermograph was located on well-drained soil in the Mixed forb-sedge community on the third and highest terrace. The Marmot hygrothermograph was located in the Mesic grass community where soils were not as well drained. This continually damp soil resulted in high relative humidity near the air-soil interface, which, in combination with characteristically low air temperatures, resulted in low VPD.

Plant production data from two plant communities at each site show that the Epilobium-Bromus community had both the highest above-ground standing crop (Table 19) and the highest rate of production (Table 20). The Marmot Snowbank community and the Wind Creek Mixed forb - sedge and Mixed forb - Salix nivalis communities had very similar seasonal trends in standing crop. Production rates were somewhat more variable, and decreased during the first phase (June and July) in the following order: Snowbank, Mixed forb - sedge, Mixed forb - Salix nivalis. Standing crop of these three communities either decreased or leveled off by early August. In contrast, the Epilobium - Bromus community continued to increase at least until the end of August. These differences can be partially explained by the position of these communities within the meadows. The Epilobium - Bromus community occupies a south-facing slope, whereas the other three are on level ground. The microclimatic significance of these topographic positions has been discussed above. The resultant effects on plant growth and

development account for much of the observed differences in plant production. Differences in species composition are also important in determining total net production, but growth rates of particular species were not investigated in this study.

Floristic differences between the sites make phenological differences difficult to interpret. Differences in time of vegetative growth, flowering and fruiting result from the particular species present as well as the microclimate. The time of snowmelt is one of the more important factors in determining phenology. Therefore any differences in meltout of the sites will have an effect on this phenomenon. For example, on May 18, 1976, the Marmot site was nearly snow-free. Only the snowbank community had significant amounts of snow. In contrast, the Wind Creek site was almost entirely covered in snow, and even two weeks later, was only ca. 50% snow-free. Therefore, initiation of spring growth at Wind Creek is significantly delayed by later snowmelt. A dramatic example of the effectiveness of snowmelt in delaying phenologic development was observed in Ranunculus eschscholtzii. This species flowers shortly after snowmelt in its characteristically moist habitat, and was flowering at both sites by the last week in May. Thirteen weeks later this same species was just beginning to flower below a permanent snowbank 1 km north of the Wind Creek site.

The shortened growing season and cooler, windier microenvironment present at Wind Creek are instrumental in determining the species capable of surviving there. Thus, floristics are highly influenced by the abiotic environment. This explains in large measure why the Wind Creek flora is more alpine than the Marmot flora.

The structure and patterning of plant communities at these sites is also very dependent on the physical environment. The species present respond individually to the complex of environmental factors operating at these sites. Most important of these factors are winter snowpack, time of snowmelt, aspect and drainage patterns. These factors combine to affect length of growing season, air temperature, soil temperature, soil moisture and evapotranspiration, all of which act directly on the performance of individual plants. Species with relatively similar response patterns to these factors will tend to occur together whenever specific habitat characteristics occur. These recurring species combinations form the nucleus of the plant communities.

Eight plant communities have been described from the two sites, with no community occurring at both. The five communities at Marmot are quite varied. Their moisture regimes range from xeric _Juniperus_ - _Arctostaphylos_ communities through several mesic communities to the Wet forb community. These communities are delimited primarily by snowmelt and drainage patterns. The three Wind Creek communities are much less diverse. All three occur on mesic, level to gently sloping terrain and are dominated by a wide assortment of forbs, sedges and grasses. Their moisture regime, which is influenced by the adjacent pond, is intermediate between the _Epilobium_ - _Bromus_ and Mesic grass communities at Marmot. However, it should not be inferred from this that habitat extremes do not occur in the Wind Creek cirque. The same gradient from xeric south-facing sites to depressional hydric sites occurs there, but has not been included in the arbitrarily delimited study site.

Floristically and structurally, the three Wind Creek sites are most closely related to the Mesic grass community at Marmot. Each of the

five communities at Marmot have been quantitatively compared to the three Wind Creek communities (Table 18). By averaging the three inter-site IS values for each Marmot community, the following decreasing order of affinity is arrived at: Mesic grass (53.24), Epilobium - Bromus (45.11), Snowbank (38.44), Juniperus - Arctostaphylos (30.14) and Wet forb (18.21). As was mentioned previously, the Mesic grass community contains species such as Astragalus alpinus and Senecio lugens which are important in Wind Creek, but absent from the other four Marmot communities. The fact that the Mesic grass community occupies a mesic, level portion of the meadow, as do the Wind Creek communities, accounts in large measure for this similarity.

The plant communities described at Marmot and Wind Creek bear little resemblance to the few subalpine plant communities described elsewhere in Canada and the United States. The Epilobium - Bromus community and the three communities at Wind Creek are somewhat similar floristically to Kuchar's (1973) Moist forb community type, but the latter appears to be intermediate between the above communities and the Mesic grass and Wet forb communities. Kuramoto and Bliss (1970) describe a Mesic grass community type from the Olympic Mountains which is environmentally similar to the Epilobium - Bromus community, but is floristically different. These authors also describe Moist Saussaurea forb and Moist Valeriana forb communities which correspond environmentally with the Wet forb community, but again floristics are very different. As on Mount Allan, several authors (Brooke et al. 1970, Kuramoto and Bliss 1970, Douglas 1972, Kuchar 1973) cite the importance of snowmelt and water table patterns in determining plant communities. Despite this environmental parallelism, species assemblages differ dramatically.

This suggests that phytogeographic and historical factors are necessary to explain observed differences. Further studies in the subalpine zone of the Canadian Rockies will be necessary to document the importance of these factors.

The soils described from Marmot and Wind Creek are best classed as Alpine Dystric Brunisols. The variability in color and horizon thickness between different plant communities indicates the influence of the environment on soil development. The effects of vegetation on the soil solum are also evident, for example, by the lower soil pH beneath Cassiope. The complex B horizons at Wind Creek present an especially interesting problem. These profiles probably result either from periodic down-slope movement of soil material or from neoglacial activity. The presence of clay in the B_1 and B_3 horizons in the Mixed forb-sedge, and B_1 horizon of the Mixed forb-Salix communities suggests a lacustrine or fluvial origin. At Marmot, the thinner horizons of the Juniperus-Arctostaphylos community reflect increased rates of erosion on topographic highs.

Just as the abiotic environment influences the vegetation and soil, it also acts both directly and indirectly on the Columbian ground squirrels at these sites. These physical factors act indirectly on the squirrels by controlling seasonal changes in plant production, phenology and distribution. Of particular importance is the initiation of the plant growing season, as food is most likely to be limiting at this time of year. Weight losses by squirrels shortly after emergence from hibernation provide evidence that this is the case (Murie 1976, pers. comm.). Another indirect effect is caused by annual differences in seed

set by plants. This variation influences the amount of dependence placed on vegetative and reproductive plant parts from year to year, and may have nutritional consequences.

The physical environment also acts directly on individual squirrels and has no doubt been an important selective force. The time of hibernation of Columbians has been correlated with differences in aspect (Shaw 1925). He found that the increased snowdepth and delayed snowmelt of northeast slopes vs. southwest slopes shifted the active season of squirrels. Hibernation, spring emergence and breeding were all approximately ten days later on northeast slopes. Time of spring emergence (and hence time of breeding and birth of young) has also been shown to be correlated with climate by Michener (1977). In a two year study, she noted early emergence in a warmer than average spring, and late emergence in a cooler than average spring. Spring emergence and emergence of juveniles from the natal burrow have been shown to be delayed with an increase in altitude and latitude (Adams 1961, Moore 1937). Similar patterns have been documented for Richardson's ground squirrels (Spermophilus richardsonii) (Clark 1970, Nellis 1969, Michener 1973) and Golden-mantled ground squirrels (S. lateralis) (Bronson 1976). Such factors as winter temperatures and snow cover may directly affect winter survival of ground squirrels. Behavioral aspects such as amount of activity and feeding have been correlated with air temperature by Betts (1976).

The environment may also act on a more complex level to influence social behavior. Barash (1974) has postulated that the degree of sociality in Marmots (genus Marmota) is a function of length of growing season and severity of the environment. The solitary woodchuck

(Marmota monax) inhabits the least severe, low elevation habitats with the longest growing seasons(e.g. 130 days in Pennsylvania (Snyder and Christian, 1960)). The Yellow-bellied marmot (M. flaviventris) studied by Armitage (1962) at mid-elevations in Wyoming shows increased sociality over the woodchuck. Its more severe environment has a growing season of only 70 to 100 days. Finally, the Olympic marmot (M. olympus) inhabits high elevation meadows in the Olympic Mountains. It is highly social, living in organized colonies where individuals do not defend territories. It has been suggested that Columbian ground squirrels also show an increase in sociality with increasing elevation (pers. comm. Michener 1976 and Kivett 1976).

But the vegetation and fauna of these subalpine meadows are not solely dependent on abiotic components. They in turn, affect micro-environment and soil characteristics, as well as each other. It was originally hoped that several potential effects of ground squirrels on vegetation could be documented in this study, and several experimental exclosures were constructed for this purpose. Unfortunately, only three squirrels inhabited the Marmot site in 1975 and did not provide the population level necessary to test this hypothesis. In fact, maximum standing crop outside exclosures (277.2 g dry wt m^{-2}) was significantly greater than inside exclosures (229.8 g dry wt m^{-2}; $p=0.05$). I feel that these differences must be attributable to factors other than squirrel herbivory. Altered microclimate is one possible explanation.

Betts (1973) provide data on the utilization of plant production by Columbian ground squirrels. He found that they consumed an average of 4.6% of net production (above-ground) over an entire season. Utiliza-

tion was lowest during the gestation period (2.6%), intermediate during the lactation period (3.2%) and highest during the post-lactation period (8.7%).

Wood (1973) assessed the overall impact of Olympic marmots on above-ground net production in a subalpine meadow in the Olympic Mountains. He estimated that total impact equalled 30.4% of total net production. This exceptionally high figure includes decreased production due to burrows and trails as well as ingestion. He did not indicate however, what proportion of this is attributable to marmots, and what proportion to other mammals, birds and insects. Based on energetics of individual marmots, he calculated independently that 17% of production is ingested. This figure is also quite high, but does indicate the important effect of marmots in subalpine meadows in the Olympic Mountains. Consumption of such a large percentage of production should be measurable in other ways. Yet Watson (1976), estimating percent cover in excluded and non-excluded plots in one of the same meadows studied by Wood (1973), could detect very few statistically significant differences. Either plant cover was not a good parameter to monitor, or marmot impact is less than reported by Wood (1973), or both. In his study of the Yellow-bellied marmot, Kilgore (cited in Betts 1973) found that 2-6.4 % of above-ground net production was consumed.

Ellison and Aldous (1952) investigated the influence of pocket gophers on subalpine grassland vegetation in central Utah. They used biomass estimates in two plots as their measure of impact. One plot was continually trapped to eliminate pocket gophers, and one was untrapped. They found little change over an eight year period, but indicated "a slight tendency for total production to increase where gophers are

present as compared with where they are absent" (p. 185).

Burrowing mammals may also affect the vegetation in other ways. Bond (1945) suggested that pocket gophers can influence plant successional processes. For instance, succession can be slowed down by the burying and trampling of plants. This will be discussed in more detail in the following chapter. Succession may also be speeded up by differential feeding on early successional tap-rooted species. This latter possibility was offered by Bond (1945) as an untested hypothesis. Range management studies have attempted to assess the beneficial or detrimental roles of several rodents, especially pocket gophers. These studies (e.g. Branson and Payne (1958), Ellison and Aldous (1952)) have tended to speak in terms of "desirable" and "undesirable" range plant species, and so do not arrive at a holistic evaluation.

These few studies at high elevations indicate, at the very least, that the importance of herbivory to plant production and structure is quite variable. Careful studies using standardized methods at suitable sites are necessary if an understanding of this factor is to be achieved.

The burrowing activities of the above mammals also have direct effects on the environment. Many of these effects have been mentioned in the literature (e.g. Grinnell 1923, Taylor 1935): soil aeration, soil churning, fertilization, structural and chemical changes, incorporation of organic materials and changes in soil moisture. These effects have not been investigated in the present study, but should be considered in any overall assessment of the "importance" or "role" of ground squirrels in subalpine habitats.

Such considerations are becoming more and more relevant in light of increased use of mountain environments. If effective management of plant and animal populations within these areas is expected, then a better understanding of ground squirrel - environment interactions is necessary. Small mammals provide an increasingly important recreational resource as more and more people come into contact with them. Effective research at this time would provide the necessary basis for future wildlife and habitat management.

BURROW MOUND VEGETATION

RESULTS

Burrow mounds of Columbian ground squirrels at Marmot range in size from negligible amounts of soil around small burrow entrances to mound "porches" up to 3.8 m^2 in area. (Porches were treated as ellipses, and area was calculated by the equation $A = \pi ab$ where a and b are the lengths of the semi-major and semi-minor axes respectively). Mean size of sampled burrow mounds was 1.27 m^2 (n = 32). These varied in aspect from 60^o to 200^o, with a mean of 130^o. It is this group of burrow mounds which provides the basis for the following results.

Previous studies of pocket gopher mounds (Laycock 1958), badger mounds (Platt 1975) and ant hills (King 1977) have shown the presence of unique species assemblages on these disturbances. Sampling of 32 Columbian ground squirrel burrow mounds at Marmot indicated no such unique species. All species occurring on mounds were also found in the surrounding meadow matrix. In contrast, only 19 (28.4%) out of 67 matrix taxa were sampled on burrow mounds.

Percent cover of these nineteen taxa was quite low ($\bar{X}$ = 2.13%). Only Epilobium angustifolium (23.8%) had a mean cover greater than 5.0%; it also had the greatest frequency, occurring on 25 of 38 mounds (65.8%). Bromus pumpellianus (63.2%) and Fragaria virginiana (52.6%) also had frequencies greater than 50%. In addition, these three species had the greatest mean densities on mounds: Epilobium (4.4), Bromus (2.8) and Fragaria (2.3). Cover, frequency and density data for burrow mounds are summarized in Table 21.

Quantitative data from mounds can also be compared to matrix data. Table 22 lists a value called "mound affinity" for each species present

Table 21. Percent frequency, mean percent cover and mean density of taxa occurring on burrow mounds, Marmot.

Species	% F	$\overline{X}$ % C	$\overline{X}$ D
Epilobium angustifolium	65.8	23.8	4.4
Bromus pumpellianus	63.2	3.1	2.8
Fragaria virginiana	52.6	5.0	2.3
Achillea millefolium	39.5	1.9	1.1
Carex spp.	31.6	1.0	-
Penstemon procerus	28.9	2.8	-
Hedysarum sulphurescens	26.3	3.2	1.1
Grasses	23.7	1.1	-
Potentilla diversifolia	13.2	0.5	0.2
Poa spp.	10.5	0.6	-
Eriogonum subalpinum	7.9	0.2	0.3
Sibbaldia procumbens	7.9	0.1	0.2
Antennaria spp.	5.3	0.4	1.2
Gentiana amarella	5.3	0.1	0.1
Cerastium arvense	5.3	0.1	0.3
Arenaria capillaris	5.3	0.1	+
Arctostaphylos uva-ursi	2.6	0.2	-
Vaccinium scoparium	2.6	0.3	0.4
Sedum lanceolatum	2.6	0.1	0.1
Draba spp.	2.6	+	+
Stellaria spp.	2.6	+	-
Mean	19.30	2.13	0.97

+ less than 0.1; - absent

Table 22. The response of meadow taxa to burrow mounds at Marmot

	Mound Affinity*	$\overline{X}$ % C on	$\overline{X}$ % C off	Frequency
Gentiana amarella	88.89	.08	.01	2
Epilobium angustifolium	66.90	23.79	11.77	25
Fragaria virginiana	63.11	5.03	2.94	20
Penstemon procerus	53.69	2.84	2.45	11
Draba spp.	50.00	.03	.03	1
Bromus pumpellianus	38.43	3.14	5.03	24
Antennaria umbrinella	37.17	.42	.71	2
Sedum lanceolatum	36.36	.08	.14	1
Cerastium arvense	35.14	.13	.24	2
Hedysarum sulphurescens	34.41	3.29	6.27	10
Achillea millefolium	25.96	1.90	5.42	15
Graminoids	16.67	2.63	13.15	20
Stellaria sp.	13.04	.03	.20	1
Vaccinium scoparium	12.62	.26	1.80	1
Sibbaldia procumbens	10.53	.06	.51	3
Potentilla diversifolia	9.41	.45	4.33	5
Eriogonum subalpinum	8.79	.24	2.49	3
Arenaria capillaris	7.21	.08	1.03	2
Arctostaphylos uva-ursi	5.56	.21	3.57	1

$$* \text{ affinity} = \frac{(\text{total \% C on mounds})\ (100)}{\substack{(\text{mean \% C off mounds})\ (\text{number of mound samples}) \\ (\text{total \% C on mounds})}}$$

modified from King (1977)

on mounds. This value indicates the tendency of a species to greater or lesser cover on mounds as compared to the matrix. Affinities greater than 50% indicate greater mean cover on mounds and affinities less than 50% indicate greater mean cover in the matrix. These mound affinities were calculated as follows:

$$\text{affinity } (\%) = \frac{\text{total \% cover on mounds}}{(\text{mean \% cover off mounds})\ (n)\ (\text{total \% cover on mounds})} \times 100$$

where n = the number of mound-quadrats (= 38)

Only four species had mound affinities greater than 50%. Gentiana amarella had the highest affinity (88.89%) but occurred on only two mounds. Epilobium angustifolium had a mound affinity of 66.90% with a mound frequency of (65.8%). Penstemon procerus (53.69%) and Fragaria virginiana (63.11%) also had affinities greater than 50%. These four species increase in abundance (as measured by cover) in response to ground squirrel borrow mounds. The remaining 15 taxa had mound affinities less than 50%, and hence were less abundant on mounds.

To test the significance of differences in relative abundance on and off burrow mounds, a Mann-Whitney U Test was performed on the seven taxa with mound frequencies $\geq$ 10. Bromus pumpellianus, Epilobium angustifolium, Hedysarum sulphurescens and Penstemon procerus showed a non-significant difference. Graminoids and Achillea millefolium were significantly ($p < 0.01$) more abundant in the meadow matrix, whereas Fragaria virginiana was significantly more abundant on the mounds.

Two pertinent questions can now be asked: 1) how uniform is the burrow mound vegetation throughout the meadow; and 2) how similar is mound vegetation to the immediately surrounding matrix vegetation? Both questions are best answered using a similarity matrix. For these

analyses, only the matrix based on Importance Values will be used (Table 23).

Since not all plant communities were widely used by ground squirrels, certain ones are not considered here, and others have been further subdivided. The Wet forb, Snowbank and Mesic grass communities are little used for burrowing and are not considered further. The *Epilobium* - *Bromus* and *Juniperus* - *Arctostaphylos* communities are used extensively for burrowing. Each of these communities was divided into four sections (I - IV; Figure 12). Burrow mounds within each section were then grouped. Four of these sections, section III of the *Juniperus* - *Arctostaphylos* community, and section II, III and IV of the *Epilobium* - *Bromus* community, had sufficient numbers of burrows to be included in this analysis. These four groups of burrows can now be compared to each other and to portions of the meadow matrix.

Uniformity of burrow mound vegetation can be examined by comparing mounds from different sections of the site. When the mean Index of Similarity (IS) of these six possible comparisons is calculated for burrow-burrow and matrix-matrix comparisons, no significant difference is found. More specifically, one can compare the one *Juniperus* - *Arctostaphylos* section with the three *Epilobium* - *Bromus* sections, thereby comparing the differing environments. Comparing burrow mounds, a mean IS value of 63.86 is calculated. The corresponding mean IS value for matrix comparisons is 51.03. Thus, a tendency toward less variability is exhibited by species assemblages on burrow mounds as compared to matrix assemblages.

The similarity between mound vegetation and the immediately

Table 23. Similarity matrix based on Importance Values. Four sections (I-IV) of the *Juniperus-Arctostaphylos* (J-A) and *Epilobium-Bromus* (E-B) communities are included. See text for interpretation.

		MATRIX										BURROW MOUNDS			
		TOT MTX	TOT BUR	J-A I	J-A II	J-A III	J-A IV	E-B I	E-B II	E-B III	E-B IV	J-A III	E-B II	E-B III	E-B IV
TOT MTX			53.84	57.31	66.15	69.76	66.25	69.20	66.49	69.65	68.14	46.90	46.39	44.47	37.75
TOT BUR				29.18	47.31	39.73	38.01	57.50	62.15	58.74	65.40	72.21	80.92	86.92	75.18
J-A I					72.99	58.41	62.48	42.28	34.65	33.22	34.71	25.28	22.87	23.47	18.78
J-A II						63.75	71.30	51.45	53.82	50.65	52.61	39.97	41.64	40.76	35.73
J-A III							79.94	46.97	49.99	52.15	50.96	35.97	32.17	34.81	29.05
J-A IV	MATRIX							46.81	46.44	47.46	47.93	33.50	31.12	32.85	30.46
E-B I									62.18	68.06	63.64	51.11	52.72	49.94	46.22
E-B II										74.43	75.17	60.96	61.57	59.84	43.54
E-B III											74.71	50.94	61.51	55.11	42.63
E-B IV												60.59	61.13	60.39	46.48

Table 23 (continued)

		BURROW MOUNDS		
		E-B II	E-B III	E-B IV
J-A III	BURROW MOUNDS	74.38	62.19	55.02
E-B II			74.72	63.99
E-B III				71.63
E-B IV				

Figure 12. Four sections of the Epilobium-Bromus and Juniperus-Arctostaphylos communities, Marmot.

surrounding matrix vegetation can be similarly analyzed. Mound-mound comparisons for the four sections have an average IS of 66.98. Matrix-matrix comparisons for these same sections average 62.90. If the burrow mounds in each of the four sections are compared with the matrix vegetation in which each is included, a mean IS value of 49.78 is calculated. This is significantly lower than the values discussed above, and only slightly higher than the mean IS value for all burrow-matrix comparisons within the study site (42.90; $n = 32$). Therefore, burrow mound species assemblages are less similar to their surrounding vegetation than one might expect.

The information above deals with plant species associations which have fluctuated over time, and in many cases have had many years to develop. But short-term events of colonization and death also occur on these mounds. In order to assess the influence of ground squirrels on these events, wire-mesh exclosures were constructed over portions of two burrow mounds which were in use during the two-year study. These excluded plots, as well as paired non-excluded plots from the same mounds were mapped four times to elucidate responses of individual plants. Figures 13 and 14 represent the distribution of individuals on these four plots at four points in time: 3 July and 27 August, 1975, and 10 July and 14 August, 1976. Despite the initially low number of individual plants, trends can be observed. Plot EX-1 (the excluded plot of pair 1) had nine individuals of Bromus pumpellianus on 3 July, 1975. On 14 August, 1976, 18 individuals of Bromus were present, including four of the original nine. Six Epilobium angustifolium plants and one Fragaria virginiana runner rooted at three places were also present. Plot NEX-1 (the non-excluded plot of pair 1) showed fewer changes over this 13.5

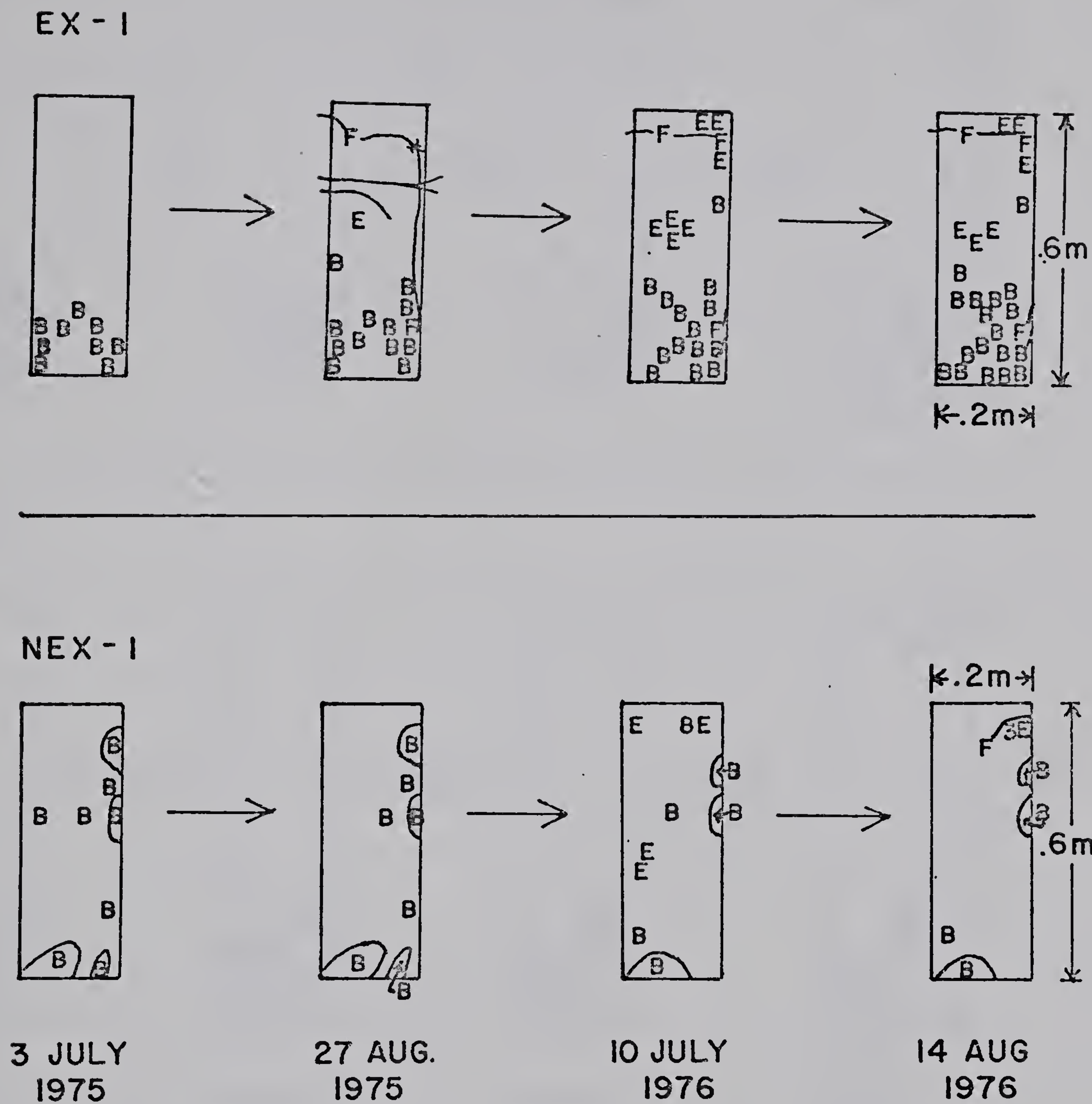


Figure 13. Location of individual plants within (EX-1) and outside of (NEX-1) a wire-mesh exclosure on burrow #1, Marmot. B = Bromus pumpellianus, F = Fragaria virginiana, E = Epilobium angustifolium.

EX-2

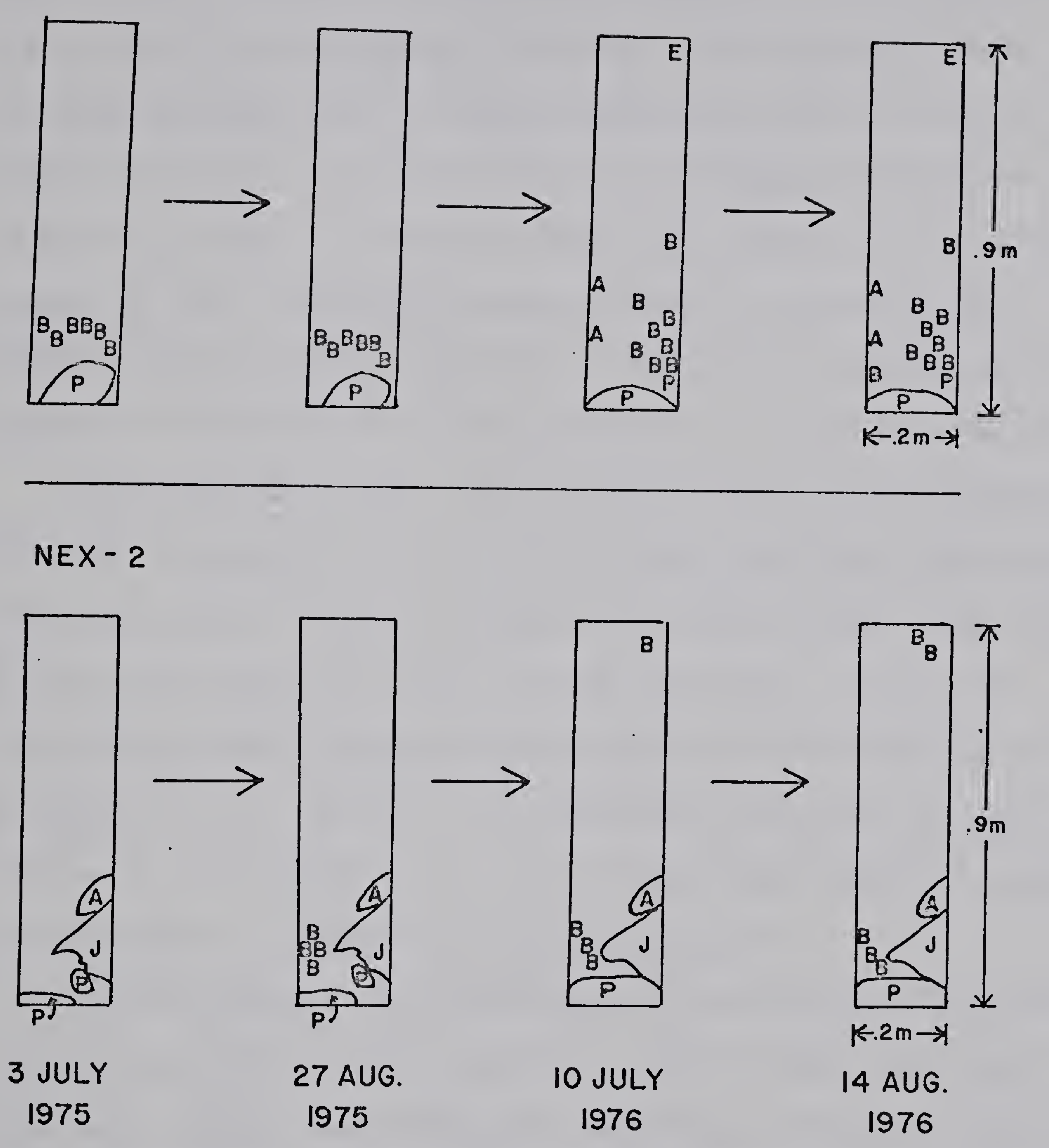


Figure 14. Location of individual plants within (EX-2) and outside of (NEX-2) a wire-mesh exclosure on burrow #2, Marmot. B = <u>Bromus pumpellianus</u>, P = <u>Penstemon procerus</u>, A = <u>Antennaria umbrinella</u>, E = <u>Epilobium angustifolium</u>, J = <u>Juniperus communis</u>.

month period. Initially, four individuals and four clumps of Bromus were present. Ultimately, the four individuals and one clump died, but were replaced by one new Bromus individual, three Epilobium plants and one rooted Fragaria runner. Based on individual plants originally present, EX-1 had a survival of 44.4% and an increase of 300% over these two growing seasons. In contrast, NEX-1 had a survival of 0% and an increase of 125%. Plots EX-2 and NEX-2 showed a similar but less dramatic trend: EX-2 had a survival of 33.3% (2 of 6 plants) and an increase of 216.7%; NEX-2 increased from 0 to 5 individuals (Figure 14).

These summaries compare numbers of individuals at the beginning and end of the experiment but do not fully present individual colonization events and deaths. Figure 15 presents these data in such a way that one can chart the success or failure of each individual. In all, 25 colonization events and seven deaths occurred in EX-1 resulting in a net change of +18. In NEX -1, 13 colonization events and 12 deaths resulted in a net change of +1. It is assumed that additional events occurred between mappings which have gone unnoticed.

Table 24 assesses the significance of survivorship differences within and outside of these exclosures. Only in 1976, when sample sizes were largest, were differences significant. When the individual probability levels are combined and tested as a group (Sokal and Rohlf 1969, p. 623), a highly significant difference in survivorship is indicated. These differences reflect the importance of ground squirrels to plant mortality.

Figure 15. Colonization events and deaths of individual plants on a ground squirrel burrow mound, Marmot. EX-1 lies within, NEX-1 outside of a wire-mesh exclosure. B = Bromus pumpellianus, F = Fragaria virginiana, E = Epilobium angustifolium.

EX-1

25 colonization events
7 deaths

$\Delta n = 18$

```
3 July 1975:    B B B B B B B B B
                ↓ ↓ ↓ ↓ ↓ ↓ ↓ ↓ ↓
27 August       B B B B B B B B B B B B F F E
1975:
                ↓ ↓ ↓ ↓             ↓ ↓   ↓ ↓ ↓
10 July 1976:   B B B B             B B   F F E B B B B B B B B F E E E E E E
                ↓ ↓ ↓ ↓             ↓ ↓   ↓ ↓ ↓ ↓ ↓ ↓ ↓ ↓ ↓ ↓ ↓ ↓ ↓ ↓ ↓ ↓ ↓
14 August       B B B B             B B   F F E B B B B B B B B F E E E E E +4B
1976:
```

NEX-1

13 colonization events
12 deaths

$\Delta n = 1$

```
3 July 1975:    B B B B
                ↓ ↓ ↓
27 August       B B B
1975:
                ↓
10 July 1976:   B         B E E E E E E E E E E E
                          ↓ ↓ ↓ ↓
14 August                 B E E E           F
1976:
```

Table 24. Chi square (X^2) and level of probability (p) for individual plant survivorship within and outside of an exclosure during five periods. Data are from Figure 16.

Period	X^2	p
3 July 1975 - 27 August 1975	2.43	0.1490
3 July 1975 - 14 August 1976	2.56	0.1259
27 August 1975 - 10 July 1976	0.71	0.4547
27 August 1975 - 14 August 1976	3.55	0.0628
10 July 1976 - 14 August 1976	18.13	<0.0050

$\Sigma \ln p < -12.8303$

$-2 \Sigma \ln p > 25.6606$ **

** significant at $p < 0.01$; see text for details

DISCUSSION

As mentioned above, several conclusions of this study differ from results obtained by other workers. Laycock (1958) investigated the initial pattern of revegetation of pocket gopher (Thomomys talpoides) mounds in Wyoming. He divided plants into those growing through mounds after burial and those germinating on mounds. Of particular importance in the latter group were annuals, accounting for 36.8% of the species (n = 19) and 95.7% of the individuals (n = 1115). The widespread occurrence of annuals on the microsites provided by these disturbances accounted for a significant increase in species richness. Douglas (1974) also noticed an increase in species richness in response to Arctic ground squirrel (Spermophilus undulatus) burrow mounds in Kluane National Park, Yukon Territory. Again, an increase in microsite diversity led to an increase in plant species richness. In this case however, annuals were not mentioned as being important.

In his investigation of badger mounds in tall-grass prairie in Iowa, Platt (1975) determined several effects of these disturbances on the vegetation. Species were divided into three groups: mature prairie species, prairie fugitives and ruderals. The first group consisted of indigenous species of the tall-grass prairie. The prairie fugitives included native species which were common on badger mounds but rare in undistrubed areas. Ruderals, or weeds, occurred in highly disturbed areas, and many were annuals and/or introduced species. The presence of the latter two groups of species which were restricted to disturbances caused an increase in species richness in virgin prairie and decreased dominance in overgrazed prairie.

King (1977) investigated the ecology of ant-hills in calcareous grasslands in England. He found several species, especially annuals, which were either much more common on, or restricted to, ant-hills. He also documented the importance of the immediately surrounding matrix vegetation in determining the composition of plant species on ant hills.

Many of these observations differ markedly from those made at Marmot. Three of the four studies discussed above cited the importance of annuals in recolonization. At Marmot, annuals are extremely rare. Of the 102 taxa present at this site, only three may sometimes behave as annuals. Equisetum pratense is limited to the Wet forb community, in which no burrow mounds occur. Androsace septentrionalis is a winter annual or short-lived perennial, and very rare at Marmot, occurring in only one quadrat in the Epilobium - Bromus community. Gentiana amarella is an annual or biennial, and is also quite rare at Marmot. It was sampled only eight times within the matrix and twice on burrow mounds. Although it does achieve greater cover on mounds, its limited occurrence renders it of minor importance to mound dynamics. Two other species, Arabis drummondii and Erigeron acris, may act as biennials, but neither were sampled on mounds. It is widely known and accepted that annuals are not an important component of alpine floras. For example, Packer (1974) states that 99% of alpine species are perennial. We can expect that annuals will also tend to be unimportant in subalpine floras.

Three species have been shown to be most important in recolonizing mounds. Epilobium angustifolium is an important component of the meadow matrix as well as of mound assemblages. This, in addition to its ability to reproduce vegetatively by rhizomes , makes it well-suited for colonizing

mounds. By spreading vegetatively in this way, portions of plants on mounds can partially overcome near-surface water deficits by conducting water from portions rooted in more mesic soil away from the mounds. Species colonizing by seed would not have this advantage. Bromus pumpellianus also has creeping rhizomes, and it also colonizes mounds vegetatively. Fragaria virginiana spreads vegetatively by means of stolons. These stolons often spread over large distances and are able to root on the exposed soil of burrow mounds. The fact that these three species spread vegetatively indicates the importance of this strategy in colonizing disturbances in the supalpine.

Because no unique species occur on burrow mounds at Marmot, the mounds do not effect species richness as compared to the meadow matrix. The underlying reasons for this can be partially explained by the nature of the subalpine environment. One important ecological function of burrow mounds is to create a disturbance within an otherwise "closed" or undisturbed plant community. This additional microsite then allows invasion by species which would otherwise not be able to become established. If however, such microsites are already available, species colonizing burrow mounds will already be present. At Marmot, additional agents of disturbance are already present. In fact, the origin of the meadow itself may date from one such agent, fire. The presence of charcoal in the soil and fire scars on nearby alpine larch attest to the previous occurrence of fire. The very presence of alpine larch may result from such fires. If fire did eliminate trees from the site, post-fire colonizing species would have become established. Further disturbances since that time may have contributed to the continued survival of those species. Such disturbances as soil frost activity, solifluction and slumping may be important in this regard. Churning of soil by frost was observed on the exposed

soil of a burrow mound. This may also occur on other areas of exposed mineral soil within the Juniperus - Arctostaphylos community. Two concave areas occur within the meadow, both situated directly above the Wet forb community. The presence of underground springs in these concavities and the presence of standing water below them during May and June suggests the possibility of slumping. Finally, the lobate nature of a large portion of the meadow suggests the possibility of solifluction as a previous or continuing process. This combination of direct (fire and soil frost activity) and indirect evidence (slumping and solifluction) lends credence to the premise that physical disturbances have been the rule rather than the exception at Marmot. It is expected then, that species capable of colonizing disturbed areas would be present even without the presence of burrow mounds. This situation, in combination with the lack of annuals, accounts for the lack of a species group occurring exclusively on burrow mounds.

The greater uniformity of burrow mound vegetation as compared to matrix vegetation is best explained in terms of the physical habitat. Burrow mounds act as "islands" within the "sea" of the matrix plant communities. Although the matrix communities vary significantly in response to aspect, drainage and snow accumulation and melt patterns, the burrow mounds are less affected by these factors. They provide a more constant environment of bare soil with more surface gravel and high surface temperatures. This relatively uniform physical environment causes less variability in the plant species assemblages occupying them.

Another aspect which has been analyzed is the dependence of species assemblages of burrow mounds on the immediately surrounding matrix vegetation. As shown by Index of Similarity values, burrow mound assemblages are no more similar to immediately surrounding vegetation than to the meadow as a whole. This differs from the conclusions reached by King (1977).

But why are there these fundamental differences between the systems described by other workers and the Columbian ground squirrel - subalpine system at Marmot? What are the underlying causes of these differences? Certainly one of the major causes is the physical environment, which has been described in the previous chapter. Even without an in-depth comparison, it is obvious that this environment differs markedly from tall-grass prairie in Iowa, chalk-grassland in England and sagebrush-bunchgrass and forest communities in Wyoming. We can expect that these differences will play a role in plant-animal interactions.

The conclusions reached regarding the effects of squirrel mounds on vegetation are based on observations made in only one meadow. Similar studies over a larger area would perhaps yield different results. Casual observations made elsewhere in the Front Ranges suggest that species richness may some times be increased by these disturbances. However, dramatic increases in richness should not be expected. Columbian ground squirrels tend to occur in greater numbers in the Main Ranges of the Canadian Rockies. Therefore, the specific direct and indirect effects on vegetation in these areas may be different.

The analysis of colonization and deaths of individuals on burrow mounds indicates a continuing and dynamic process. Despite the significant number of colonization events, burrow mounds remain unvegetated for apparently long periods of time. This can be partially explained by the effects of the physical environment on survival of individuals. The increased number of successful colonizations within exclosures suggests that additional factors are involved. Although these exclosures effectively exclude all vertebrates, it is the Columbian ground squirrel which is the most important resident of this meadow. It can be safely assumed then, that a major source of plant mortality on burrow mounds is burying,

trampling and consumption by ground squirrels. Each of these mortality sources was observed by the author. The pattern exhibited by EX-1 probably presents an accurate picture of mound colonization events. In the absence of such exclosures however, these individuals would normally be eliminated by the squirrels as shown by NEX-1 (Figure 13). As burrow mounds are abondoned by squirrels, colonizations by plants would remain relatively constant but mortality would decrease, leading to a slow but steady revegetation of burrow mounds. But many years appear to be necessary to achieve 100% plant cover. The reoccupation of abondoned mounds by squirrels would interrupt revegetation, perhaps reverting the system to a mound of bare soil. This cyclic process is continual, and can be found in all stages of development at the Marmot site.

This cyclic phenomenon appears to be common to many natural agents of disturbance. Other burrowing mammals such as pocket gophers, marmots, badgers and other ground squirrels also cause cyclic patterns of vegetation development (succession) and destruction. Such patterns have been documented by Osburn (1958) for pocket gophers (_Thomomys talpoides_) on Niwot Ridge, Colorado, by Klikoff (1965) for Belding ground squirrels (_Spermophilus beldingi beldingi_) and pocket gophers (_Thomomys monticola monticola_) in the Sierra Nevada, California and by Johnson and Billings (1962) for pocket gophers (_T. talpoides_) on the Beartooth Plateau of Wyoming. Many types of physical disturbance cause similar cyclic patterns to occur. Bryant and Scheinberg (1970) have shown this to be the case for soil frost action on Plateau Mountain, Alberta. Wildfire in coniferous forest also causes cyclic patterns of secondary succession (e.g. Heinselman 1973). Other agents of disturbance such as avalanches, blowouts and flooding would have similar ecologic effects. The results of such action are several:

habitat diversity is increased by causing a mosaic or patchwork over space, plant and animal populations are influenced over space and time and cycling of nutrients in space (e.g. through soil churning) and time is modified. These very important ecologic effects are sometimes obvious, sometimes subtle, but should not be overlooked in any assessment of the "importance" or "role" of Columbian ground squirrels (or any other disturbance) in their habitat.

INTEGRATION

Observations and measurements of various components of the physical environment have provided an understanding of microclimate and habitat patterns at Marmot and Wind Creek. These patterns have provided explanations for differences in plant communities, plant production and phenology both between and within sites.

Because both meadows were at an elevation of 2225m, on reworked shale of the Kootenay Formation, the complex environmental factors of elevation and parent geologic material have been held constant. This has allowed a more meaningful interpretation of those factors which did differ between the two sites. An analysis of air temperature, wind, precipitation, global radiation and vapor pressure deficit has led to the following conclusions:

(1) Wind Creek is cooler and windier than Marmot.

(2) Summer precipitation does not differ between the two sites.

(3) Radiation is greater at Marmot due to decreased cloud cover and less shading by surrounding landforms.

(4) Vapor pressure deficit is greater at Wind Creek, a result of hygrothermograph position in the meadows.

These microclimatic factors act in conjunction with winter snowdepth, summer snowmelt, aspect and drainage patterns to account for differences in plant communities, plant production and phenology. The influence of these factors is especially evident at Marmot where a wider range of sites was included for study. Late snowmelt at the western end of the site largely accounts for the presence of the Snowbank commu-

nity there. Standing water in depressional areas is the major reason for the presence of the Wet forb community. Exposed ridgetop positions receive increased radiation and are subject to increased erosion. These areas support the xeric Juniperus - Arctostaphylos community. Well-drained, south-facing slopes support a more mesic Epilobium - Bromus community which has the highest standing crop and rate of plant production. A level area adjacent the Wet forb community supports a Mesic grass community whose moisture regime is intermediate between the Epilobium - Bromus and Wet forb communities. Of the five communities delimited at Marmot, the Mesic grass community is the most similar floristically and structurally to the three Wind Creek communities. This results primarily from their similar topographic positions and moisture regimes.

Soils at these sites also reflect environmental differences. Soil profiles at Wind Creek are deeper and more complex. They also tend to have a coarser texture, but structure and consistency are quite similar.

Quantitative sampling of species assemblages on burrow mounds allowed the following conclusions:

(1) Very few species are important in colonizing these mounds. Although seven taxa (Epilobium angustifolium, Bromus pumpellianus, Fragaria virginiana, Achillea millefolium, Carex spp., Hedysarum sulphurescens and Penstemon procerus) had frequencies greater than 25%, only Epilobium had a mean cover greater than 5% (23.8%).

(2) Annuals are not important in colonizing burrow mounds. Vegetative reproduction by rhizomes is the most important means of colonization.

(3) Only Gentiana amarella, Epilobium, Penstemon and Fragaria had higher mean per cent cover on the mounds than off.

(4) Species assemblages on burrow mounds are less variable than are those of the surrounding meadow matrix.

(5) Species assemblages on burrow mounds are not floristically dependent on the plant community in which they occur.

(6) Individual colonization events take place regularly, but few of these plants survive the burying, trampling and herbivory of Columbian ground squirrels.

Experimental exclosures constructed to assess the impact of Columbians on net production indicated that this was negligible at Marmot in 1975. This suggested that burrowing and digging activities were more important ecologically in these meadows. These activities provide additional sites for species already present in the meadow matrix. Direct effects on the soil can also be expected to result from these activities. Such results as mixing of horizons, increased soil aeration, creation of microhabitats suitable for bryophytes and soil invertebrates, incorporation of organic matter below the Ah horizon (fecal and nesting material) and modification of soil chemistry can be expected to have effects on both the vegetation and on other animals.

All these processes are part of the overall impact of Columbian ground squirrels in their subalpine habitat. They are an integral part of the cyclic changes caused by periodic occupation and abandonment of particular burrow complexes or portions of these meadows. This cyclic phenomenon has been shown to be similar to the actions of other natural agents of disturbance such as fire, soil frost activity, flooding and

avalanche. It is suggested that these cyclic activities are both a natural and necessary function of most ecosystems.

These many obvious and subtle effects of Columbian ground squirrels in subalpine environments have been little studied. The dramatic increase in the use of mountain environments in recent years suggests that environmental alteration by man is a certainty. If we make the reasonable assumption that the presence of Columbian ground squirrels is desirable in these environments, then a better understanding of their relationship with their abiotic and biotic surroundings is necessary. Only then can we make intelligent management decisions concerning maintenance of habitats and wildlife populations.

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APPENDIX I

Species and Importance Values in five plant communities at Marmot and three plant communities at Wind Creek.

Species	Marmot E-B	J-A	Wf	Sn	Mg	Wind Creek PAs	Mfs	Mfsx
Ophioglossaceae								
Botrychium boreale *	1.16	0.39		1.67		0.69		
B. lunaria								
Equisetaceae								
Equisetum pratense	1.48				5.85			
Selaginellaceae								
Selaginella densa	0.68	3.44		9.77				
Pinaceae								
Abies lasiocarpa		1.81		4.28		WC ***		
Juniperus communis var. depressa		48.74		3.29		WC		
J. horizontalis	0.23	7.79						
Larix lyallii					0.90			
Picea engelmanii		0.17				WC		
Gramineae								
Graminoids **	29.02	14.98	14.81	16.65	31.48	26.64	20.09	22.12
Agropyron latiglume	M							
Bromus pumpellianus	17.62	7.20	2.84	6.32	19.13			
Calamagrostis sp.	M							
Alopecurus occidentalis	M							
Elymus innovatus	M					WC		
Phleum alpinum	M					WC		
Poa alpina	M					WC		
P. grayana	M							
Cyperaceae								
Carex albo-nigra	M							
C. atrata *	M							
C. phaeocephala	M					WC		
C. rupestris						WC		
C. xerantica	M							
Kobresia bellardii						WC		
Juncaceae								
Juncus drummondii	M					WC		
Luzula multiflora						WC		
L. spicata	M							

Appendix I continued

Species	Marmot					Wind Creek		
	E-B	J-A	Wf	Sn	Mg	PAs	Mfs	Mfsx
Liliaceae								
Allium cernuum	1.00							
Salicaceae								
Salix arctica							2.20	
S. barratiana								6.39
S. drummondiana						8.43		
S. glauca	0.23				0.90	WC		
S. nivalis						1.60	2.04	13.21
Polygonaceae								
Eriogonum subalpinum	4.39	5.50		7.56				
Oxyria digyna			30.83					
Polygonum viviparum	0.26					2.90	2.88	5.28
Rumex alpestris	1.00	0.13			3.84	7.09	6.95	6.70
Portulacaceae								
Claytonia lanceolata	M							
Caryophyllaceae								
Arenaria capillaris	2.20	4.46		16.56		2.22		10.17
A. obtusiloba						WC***		
A. rubella	0.13							
Cerastium arvense	2.74	1.96			0.71	8.17	11.03	7.52
Lychnis drummondii				0.88				
Silene acaulis								6.39
Stellaria longifolia *S. longipes*	0.34	0.13	15.26		4.27	6.58	10.67	1.76
Ranunculaceae								
Anemone drummondii *A. multifida* *A. occidentalis* *A. parviflora*	0.12	0.97	2.39	1.96				1.60
A. patens	M							
Aquilegia flavescens							1.86	
Delphinium bicolor	0.85	0.69						
D. glaucum			7.99			WC		
Ranunculus eschscholtzii	M					1.45	1.69	1.60
Thalictrum occidentale	M							
Trollius albiflorus	M							
Cruciferae								
Arabis drummondii	M							
A. lyallii	M					WC		
Draba albertina						WC		
Draba aurea *D. borealis*	0.63	0.53				WC		

Appendix I continued

Species	Marmot					Wind Creek		
	E-B	J-A	Wf	Sn	Mg	PAs	Mfs	Mfsx
Draba incerta	M					WC		
D. oligosperma						WC		
Smelowskia calycina var. *americana*							1.52	
Crassulaceae								
Sedum lanceolatum		4.44		2.15		6.65	3.06	1.76
S. rosea					2.63	WC		
Saxifragaceae								
Saxifraga bronchialis		7.96		1.29		WC		
S. caespitosa						WC		
S. occidentalis		0.14						
Rosaceae								
Dryas octopetala	M					WC		
Fragaria virginiana	10.43	2.59			3.38			
Potentilla diversifolia	14.04	9.91	3.99	16.49	16.00	25.26	22.97	24.93
P. fruticosa	M							
P. nivea	M							
P. uniflora						WC		
P. villosa	M							
Sibbaldia procumbens	0.53	1.71		9.81		8.16		7.93
Leguminosae								
Astragalus alpinus	1.22				7.04	15.14	17.85	18.87
A. occidentalis	M							
Hedysarum sulphurescens	16.40	3.10		1.43	15.19	2.14		
Oxytropis podocarpa	M							
Onagraceae								
Epilobium alpinum		0.13						
E. angustifolium	26.62	11.56	39.41	14.21	5.85	WC		
E. glandulosum			2.39					
Umbelliferae								
Heracleum lanatum	M							
Ericaceae								
Arctostaphylos uva-ursi	0.23	15.03						
Cassiope tetragona						WC		
Phyllodoce glanduliflora						WC		
Vaccinium scoparium	1.45	7.65		16.27				
Primulaceae								
Androsace chamaejasme						WC		
A. septentrionalis	0.11					1.52	3.23	1.45
Dodecatheon conjugens	M							
D. radicatum	M							

Appendix I continued

Species	Marmot					Wind Creek		
	E-B	J-A	Wf	Sn	Mg	PAs	Mfs	Mfsx
Gentianaceae								
Gentiana amarella	0.48	0.26		0.82		2.14		
Gentiana sp.						WC		
Polemoniaceae								
Polemonium pulcherrimum	M					0.83		
Hydrophyllaceae								
Phacelia sericea		0.20						
Boraginaceae								
Hackelia jessicae	M							
Myosotis alpestris	2.87	1.00			7.44	9.84	11.70	3.19
Scrophulariaceae								
*Besseya wyomingensis**	0.13						1.69	
Castilleja occidentalis	M					WC		
Castilleja sp.						WC		
Pedicularis contorta	0.62	0.67		7.94				
Penstemon procerus	10.22	5.41		1.21	3.45	4.96	4.58	4.86
Veronica wormskjoldii *	1.76			1.28		3.74	1.37	1.93
Rubiaceae								
Galium boreale	1.60	0.29			11.06			
Valerianaceae								
Valeriana sitchensis	1.59		9.45	5.72				
Campanulaceae								
Campanula rotundifolia	2.03	3.44		1.48	2.04	WC		
Compositae								
Achillea millefolium	17.21	9.99	14.23	11.96	20.86	22.49	23.31	18.48
Agoseris aurantiaca	0.86	0.46		0.61				
Agoseris glauca	0.40				1.27	3.82		
Antennaria alpina						WC		
Antennaria lanata }	1.28	3.28		11.41				6.00
A. umbrinella								2.59
Arnica cordifolia	0.40	1.00						
A. alpina						WC		
Arnica sp.	0.69	0.17		2.89	0.67			
Erigeron acris				0.41		WC		
E. aureus	M					WC		
E. humilis						WC		
E. peregrinus	12.39	1.38	26.59	5.80	4.29	8.56		
Senecio lugens					4.29	3.28	12.41	6.44
S. triangularis			29.80					
Solidago multiradiata	9.36	9.36		17.90	24.55	6.03	19.56	12.10
Taraxacum ceratophorum	0.27				2.88			

Appendix I continued

Bryophyte species	Marmot	Wind Creek
Ditrichaceae		
Ceratodon purpureus	X****	X
Dicranaceae		
Dicranum scoparium		X
Encalyptaceae		
Encalypta rhaptocarpa	X	
Encalypta sp.	X	
Pottiaceae		
Desmatodon latifolius	X	X
Tortula norvegica		X
Tortula ruralis	X	X
Grimmiaceae		
Grimmia affinis	X	
G. apocarpa	X	
Rhacomitrium canescens var. *ericoides*	X	
Bryaceae		
Bryum lisae var. *cuspidatum*	X	
B. pseudotriquetrum	X	X
Pohlia cruda	X	
P. nutans	X	X
Mniaceae		
Mnium lycopodioides	X	
Leskeaceae		
Pseudoleskea sp.	X	
Thuidium abietinum	X	
Amblystegiaceae		
Drepanocladus sp.		X
Brachytheciaceae		
Brachythecium sp.	X	
Eurhynchium pulchellum	X	
Hypnaceae		
Hypnum revolutum	X	
Isopterygium sp.	X	
Polytrichaceae		
Polytrichum juniperinum	X	X

Appendix I continued

Bryophyte species	Marmot	Wind Creek
Lophoziaceae		
Barbilophozia hatcheri	X ****	
Marchantiaceae		
Marchantia sp.		X
Lichen species		
Peltigeraceae		
Peltigera canina	X	X
Solorina crocea	X	
Stereocaulaceae		
Stereocaulon alpinum	X	X
Cladoniaceae		
Cladonia chlorophaea	X	
Parmeliaceae		
Cetraria cucullata	X	X
C. ericetorum	X	X
C. nivalis	X	X
C. tilesii		X
Parmelia sp.	X	
Usneaceae		
Thamnolia subuliformis		X
Thamnolia vermicularis	X	

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* nomenclature after Hitchcock and Cronquist (1973)
** includes grasses and sedges, exclusive of *Bromus pumpellianus*
*** M = present at Marmot; WC = present at Wind Creek
**** X = present

E-B (*Epilobium-Bromus*); J-A (*Juniperus-Arctostaphylos*); Wf (Wet forb); Sn (Snowbank); Mg (Mesic grass); PAs (*Potentilla-Achillea*-sedge); Mfs (Mixed forb-sedge); Mfsx (Mixed forb-*Salix nivalis*).